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RELATIONSHIPS
IN THE CHARADRII (SHOREBIRDS):
A TAXONOMIC STUDY
BASED ON COLOR PATTERNS
OF THE DOWNY YOUNG

JOSEPH R. JEHL, JR.

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INTRODUCTION

The avian order Charadriiformes is composed of three suborders: Charadrii, Lari, and Alcae. By far the largest and most diversified of these is the Charadrii (shorebirds or waders), in which seven superfamilies, 12 families, and over 200 species are currently recognized (Peters, 1934). Since the late Cretaceous this group has undergone an extensive degree of adaptive radiation, particularly in bill morphology, which equals or surpasses that found in any other avian suborder. The major shorebird lines, currently recognized as families, are distinguished largely by differences in bill shape. In most cases the allocation of species to families, subfamilies, and genera is well established. However, the interrelationships of these higher taxa are inadequately known, as shown by the variety of classifications that have been proposed in recent years (e.g., Lowe, 1931b; Peters, 1934; von Boetticher, 1934; Mayr and Amadon, 1951; Verheyen, 1958a; Yudin, 1965; Brodkorb, 1967). Most of these classifications have been based largely on P. R. Lowe's extensive studies of the Charadrii and their close relatives in the Gruiformes. Lowe studied many characters, but he placed greatest emphasis on the morphology of the bill and skull. Consequently, his work was primarily valuable in emphasizing lines of divergence, but not in clarifying interrelationships within the Charadrii.

In this study I have attempted to reassess interrelationships in the Charadrii by analyzing variation in the downy plumage. Plumage patterns of adult birds probably have been used more often than any other character in inferring relationships at the generic level, and sometimes above. However, chick patterns have been largely ignored, even though in some taxa (e.g., Anatidae: Delacour and Mayr, 1945; Tetraoninae: Short, 1967; Podicipedidae: Storer, 1967) they have proved valuable in suggesting or confirming relationships. Recognition of the potential taxonomic value of shorebird chick plumages is not original. It was first noted by Lowe (1915) and subsequently by Ticehurst (1933) and Verheyen (1958a). Unfortunately, these workers, perhaps handicapped by inadequate material, made no more than preliminary attempts to study chick plumages, and the results of their investigations played only a minor and sometimes inconsistent role in their classifications. Since

downy plumages have not been fully utilized previously, and since, in general, there is no important correlation between adult and chick plumage patterns, except in the plover genus *Charadrius*, (see p. 32), the downy plumages can be used as an essentially independent means of evaluating relationships in this suborder.

A method for investigating the taxonomic significance of a single character or character complex has been outlined by Bock (1960: 363-364). Briefly: 1) the occurrence, structure, and variation of the character is studied, 2) its functional significance is determined, and 3) its evolution is postulated. As Bock has emphasized (p. 364), understanding the functional significance is the most important part of the investigation, for with this knowledge "one can estimate the selection forces which were operative during the evolution of the character. A knowledge of the selection forces is essential because while it is possible to outline the phylogeny of a structure without knowing the selection forces, it is impossible to understand its evolution without them." With this information the taxonomic value of the character can be evaluated.

The downy plumage of shorebird chicks is best considered as a character complex consisting of four partially independent characters: color, color pattern (or pattern), feather structure, and patterning of individual feathers. For reasons discussed below I have placed greatest emphasis on the relationships indicated by color pattern. The color of young shorebirds seems to be strongly correlated with that of the substrate in nesting areas (Cott, 1957: 124-131); for this reason it is usually of little taxonomic value. Feather structure and patterning of individual feathers, in general, show too little variation to be of wide usefulness; however, some significant exceptions occur, and those considered taxonomically important are discussed. Some types of feather structure may result from convergence; for example, the down of arctic species is long and densely barbed, whereas that of temperate-zone forms is shorter and more sparsely barbed. Convergence in patterning of individual feathers, e.g., the white-tipped dorsal down of *Thinocorus*, *Oreopholus*, *Calidris*, and *Cursorius*, also occurs.

In this study I examined chicks of 109 of the 201 shorebird species and photographs or descriptions of 53 additional species. The number of genera examined is a more important criterion of completeness, however, because there is little intrageneric pattern variation. Chicks of 41 of the 56 genera recognized here were available; descriptions or photographs were available for all others except *Microparra* (Jacanidae), *Pluvianellus* (Charadriidae), and *Prosobonia* (Scolopacidae). The absence of significant intraspecific plumage variation obviated the use of large series, but several specimens of each species were examined if possible, for even in the most carefully prepared skins the patterns are easily disarranged. For maximum value in future studies field workers are encouraged to prepare chicks of all ptilopaedic species as shown for *Charadrius semipalmatus* (Fig. 7).

Specimens were borrowed from the British Museum (Natural History), Carnegie Museum, Chicago Natural History Museum, Museum of Comparative Zoology, Museum of Vertebrate Zoology, National Museum of Canada, Royal Ontario Mu-

seum, George M. Sutton, and David F. Parmelee. In addition I examined the entire collections of shorebird chicks in the following institutions: American Museum of Natural History, The University of Michigan Museum of Zoology, the San Diego Natural History Museum, and the United States National Museum. Living chicks of 19 species were also studied.

Misidentified specimens pose a potentially serious problem in a study of this type. Several were detected once the degree of intraspecific and intrageneric variation was known; in each case the confusion was with a sympatric species. Possible errors in identification to species, though not to genus, may still exist for species in which only a single chick was examined. However, from consideration of previously published descriptions, geographic locality of the specimen, reliability of the collector, and the fact that chicks of most species are distinguishable, the possibility seems unlikely.

Observations on the functional significance of chick plumages were made at Churchill, Manitoba, Canada, in the summers of 1964, 1965, and 1966.

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COLOR PATTERN AS A TAXONOMIC CHARACTER

It is not at all obvious why chick patterns should be expected to yield satisfactory taxonomic information. Delacour and Mayr (1945: 4) justified their use by terming them "non-adaptive" characters. However, in nearly all animals a high percentage of the annual mortality occurs among the very young, and any characteristics that minimize this loss will be of selective advantage. In shorebirds, and perhaps in all groups with precocial young, the plumage patterns are cryptic or disruptive and function to reduce the chicks' conspicuousness (Cott, 1957: 54, 60-61, Fig. 14, Pl. 19). Thus, pattern *per se* must be considered adaptive even though several patterns may appear to be of similar selective value in a particular habitat (see below).

Several persons have suggested to me that chick patterns might also aid the parents to recognize their young, but this does not seem to be the case in any species I have studied in the field (*Charadrius semipalmatus*, *Pluvialis dominica*, *Numenius phaeopus*, *Limosa haemastica*, *Tringa flavipes*, *Limnodromus griseus*, *Gallinago gallinago*, *Calidris pusilla*, *C. minutilla*, *C. alpina*, *Micropalama himantopus*, *Phalaropus lobatus*). Chicks of these species are often obscured from the parents' sight by vegetation, and maintenance of the family group appears to be accomplished primarily, if not entirely, through vocalizations. The absence of "character displacement" in chick plumages of closely related sympatric species, and the observation that some shorebird species may attend other than their own young (Parmelee, Greiner, and Gaul, 1968: 20-21; Jehl, pers. obs.), further indicates that visual recognition may be of minor importance.

CONSERVATISM OF PLUMAGE PATTERNS

In spite of their adaptive role, downy patterns appear to be highly conservative and to reflect phylogenetic relationships and not environmental differences for the following reasons:

1) The patterns are restricted to the Charadrii and do not occur in groups thought to be closely allied to this suborder.

2) Patterns show little variation within species, genera, and sometimes within higher taxa.

3) Patterns are similar in closely related genera.

4) The young of closely related species occupying different habitats possess similar downy patterns. For example, in North America, *Haematopus palliatus* nests on sandy beaches, whereas *H. bachmani* nests on rocky shores; the patterns, though not the coloration, of their chicks are identical. In Europe, *H. ostralegus* nests "on or near shore, on shingle beds, among rocks, in sand dunes, or among grassy banks" (Witherby et al., 1940: 416); there is no intraspecific pattern variation in this species.

5) The young of distantly related species occupying the same habitats at the same time possess differing downy patterns. For example, in wet marshes at Churchill, Manitoba, in early July, the similarly-colored grayish chicks of *Numenius phaeopus*, *Limosa haemastica*, and *Tringa flavipes* are present; three distinct color patterns are represented by their plumages. In the same marsh occur the brownish chicks of *Limnodromus griseus*, *Gallinago gallinago*, *Calidris minutilla*, *C. alpina*, *C. pusilla*, *Micropalama himantopus*, and *Phalaropus lobatus*; three additional color patterns are represented. In addition, young of *Branta canadensis*, *Anas actua*, *Coturnicops noveboracensis*, and *Lagopus lagopus* (four additional patterns) are often present. Many additional examples could be advanced.

I know of no instance in which the presence of similar or identical color patterns should be attributed to convergence. In many groups patterns are so complex that the independent evolution of similar patterns seems highly improbable. Furthermore, the precise configuration of patterns is not usually obvious in living chicks; for example, "diamond-shaped" patterns on the lower back of curlews and godwits can rarely be discerned, but appear as a random mixing of dark and light down. Thus, it cannot be argued that similarities reflect selection for specific patterns. An exception must be made in the case of *pattern loss*, which has occurred in many unrelated forms, notably species nesting along mountain streams or on uniformly colored substrates, e.g., *Ibidorhyncha*, *Phegornis*, *Heteroscelus*, *Cladorhynchus*.

I would conclude from the above that shorebird chick patterns are conservative, that different patterns may be adaptive in similar habitats, and that

some patterns may be adaptive in a variety of habitats.

EXPERIMENTAL DATA

It would be desirable to provide experimental evidence for the adaptive equivalence of downy plumage patterns in different habitats. Unfortunately, selection experiments with nidifugous chicks are extremely difficult to perform under natural conditions; the survivorship of individual species cannot be measured precisely, nor can sufficient natural predation on the chicks be observed. However, a crude predation experiment was attempted. Specimens of seven species of waders (*Pluvialis dominica*, *Tringa flavipes*, *Actitis macularia*, *Scolopax minor*, *Gallinago gallinago*, *Calidris alpina*, *Phalaropus lobatus*), and one grouse (*Lagopus lagopus*), each with a different color pattern, were photographed on the substrates in several different types of habitat (Fig. 1). At Churchill, Manitoba, these included a wet marsh, a dry marsh, and a lichen-covered hillock; at Ann Arbor, Michigan, a deciduous woods. Photographs

were taken in color, from a uniform height, and within 30 feet of a nest of one of the species or in areas where chicks of at least one species were known to occur regularly. From one to eight specimens were included in each picture. Twenty-one such photographs were then viewed by ten persons, in most cases graduate students in ornithology, previously familiar with downy plumages of the species involved. These "predators" examined each slide for a period of 20 seconds, during which they were asked to indicate the approximate location of chicks in the order in which they were found by marking "1", "2", etc., on prepared forms. The short viewing time insured that the less-conspicuous chicks would be overlooked.

The results of this experiment could not be quantified and therefore must be regarded as inconclusive. Variation in conspicuousness of chicks resulting from unevenness of topography, relative size of the specimens, "make" of the skin, and position of the specimen in the photograph, and so forth, precluded any constancy between pictures. However, by determining for each picture which chicks were *not found* or were found only with great difficulty, I subjectively evaluated the con-

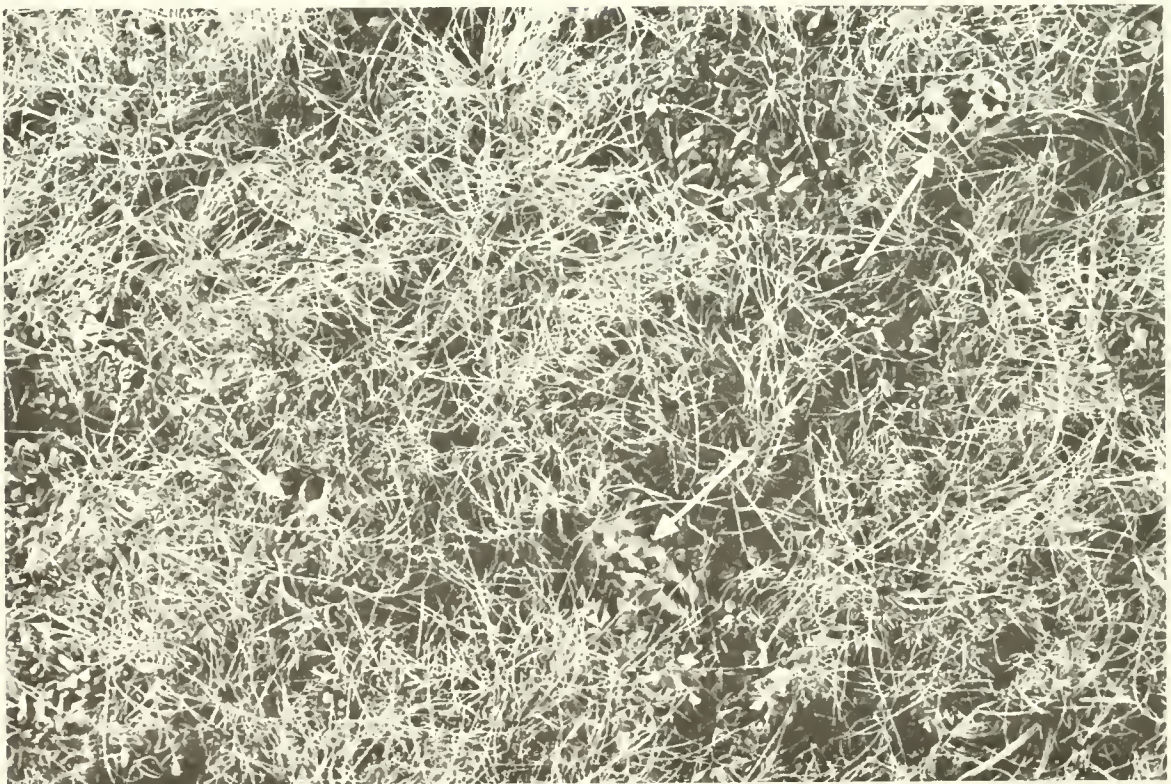


Fig. 1. Specimens of downy young photographed in a dry marsh at Churchill, Manitoba. Left to right: *Phalaropus lobatus*, *Tringa flavipes*, *Scolopax minor*.

spicuousness of chicks in each habitat. It appeared that chicks of *Tringa flavipes*, *Actitis macularia*, *Gallinago gallinago*, *Calidris alpina*, and *Phalaropus lobatus* were relatively inconspicuous on all substrates. The *Pluvialis dominica* chick was highly conspicuous in the dry tundra marsh and in the deciduous woods, the *Scolopax minor* chick on the lichen-covered hillock. The *Lagopus lagopus* specimen was inconspicuous on all substrates at Churchill, but was not tested in deciduous woods. Thus, the results of this artificial experiment suggest that some patterns may be concealing in a variety of habitats and that different patterns may

be concealing in the same habitat. Workers who may wish to conduct similar experiments should consider the following improvements in technique: 1) specimens should be approximately the same size and should be prepared to simulate the normal crouching position of chicks; 2) legs of specimens are particularly conspicuous and should be removed or folded to lie under the body; 3) photographs should be taken on black-and-white and on color film so that the concealing effects of pattern as well as coloration can be differentiated; 4) the effect that the specimen's position in the photograph has on its conspicuousness should be examined.

COLOR PATTERNS OF SHOREBIRD CHICKS

Chick color patterns are described below for each genus and the extent of intrageneric variation is noted; representatives of many genera are illustrated and the major variations in pattern are diagrammed. In most cases the diagrams are composites made from the examination of several specimens, but whenever possible they were drawn from living chicks. In interpreting the diagrams, greatest emphasis should be placed on the prominent back and head markings; minor markings on the face, back, and wings are variable and seem to be of no taxonomic importance. Before making interpretations the reader should compare the diagrams with the photographs, for complete reliance on the diagrammed patterns could lead to error; chicks of *Limosa* and *Calidris*, for example, are far more different than the diagrams alone can indicate.

No attempt has been made to provide detailed descriptions of the downy plumages for individual species, since adequate descriptions of most species already exist. However, original descriptions are given in the Appendix for species that have not been described previously or for which the published descriptions are inadequate.

The classification followed is basically that of Peters (1934), the last revisor of the entire suborder; minor departures are noted in the text. Since the appearance of Peters' classification several generic mergings have been proposed. I advocate those discussed below.

1) Bock's (1958) generic classification of the Charadriidae is followed, except, as discussed below, *Oreopholus* is considered distinct from *Eudromias*.

2) *Aechmorrhynchus* is merged with *Prosobonia*

for reasons that will be discussed elsewhere (Zusi and Jehl, in prep.).

3) *Pseudototanus* is merged with *Tringa*. This merging has been suggested by several workers (e.g., Vaurie, 1965); I consider the characters listed by Hume (1876: 345-347; 1878: 489) insufficient to support generic distinctness.

4) I follow De Schauensee (1966) in merging *Chubbia* with *Gallinago*.

5) Peters (1934) and others have classified the woodcocks in two genera, *Scolopax* and *Philohela*, the latter containing only one species, *minor*. Characters used to differentiate *Philohela* include: 1) the more rounded tail, which contains 14 instead of 12 rectrices and in which the outer rectrices are narrowed, 2) the attenuation of the outer three primaries, and 3) the eutaxic condition of the secondaries (Ridgway, 1919; Miller, 1915). In addition, the courtship displays of *Philohela* differ from those of *Scolopax rusticola*.

In my opinion these points do not justify the continued generic recognition of *Philohela*. Variation in tail shape and in the number of rectrices also occurs, and to a much greater extent, in *Gallinago* (Baker, 1929: 265, Pl. 3), a genus that is usually assumed closely allied to *Scolopax*. The configuration of the primaries is associated with courtship behavior, the attenuated feathers being used to make mechanical sounds during the courtship flight (Pettingill, 1936: 288). *Philohela* is the only reported eutaxic sandpiper, but variation within other families, genera, or even a single individual is known (Miller, 1915, 1924; Verheyen, 1958b). The taxonomic significance of this condition is debatable, but since eutaxy is usually associated with a short-winged condition in other groups, it is

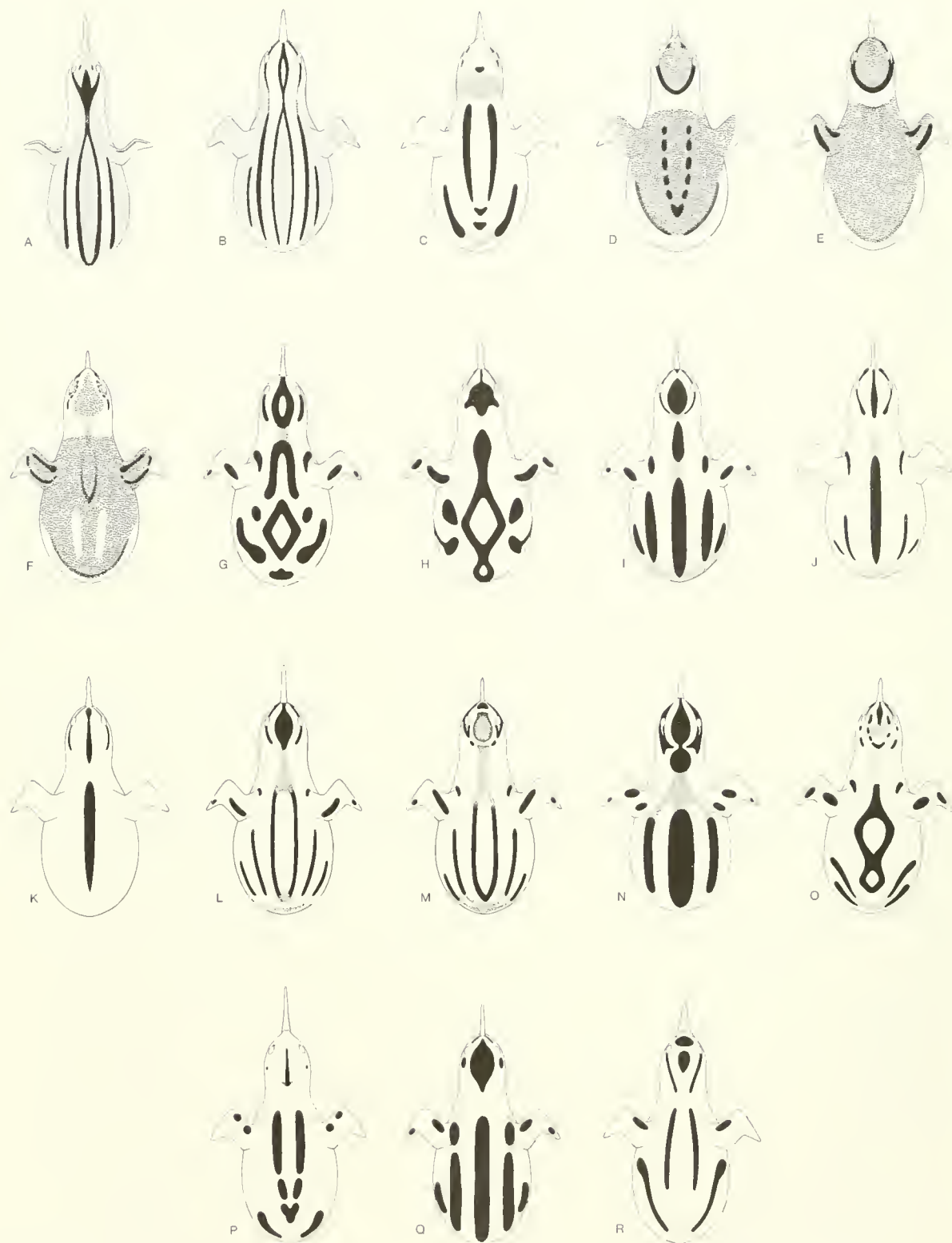


Fig. 2. Pattern diagrams of: A. *Actophilornis africana*; B. *Rostratula benghalensis*; C. *Haematopus palliatus*; D. *Vanellus duvaucelii*; E. *Charadrius semipalmatus*; F. *Pluvialis dominica*; G. *Numenius phaeopus*; H. *Limosa haemastica*; I. *Tringa flavipes*; J. *Xenus cinereus*; K. *Actitis macularia*; L. *Limnodromus griseus*; M. *Gallinago gallinago*; N. *Scolopax minor*; O. *Calidris ptilocnemis*; P. *Himantopus himantopus*; Q. *Phalaropus lobatus*; R. *Burhinus oedicnemus*.

not especially surprising to find it appearing in this relatively short-winged group of sandpipers. The significance of the courtship differences cannot be evaluated, for courtship displays have been described for only *minor* and *rusticola* (Pettingill, 1936; Steinfatt, 1938). However, the differences between these species are no greater than differences within *Gallinago* or *Calidris*.

All the differences noted may be correlated with breeding behavior. The epigamic role of the primaries has been noted; the rectrices are also used by the males in courtship (Pettingill, 1936: 295-296) and by the females in distraction displays (Pettingill, 1936: 332; pers. obs.); a possible functional relationship between eutaxy and the attenuated condition of the primaries deserves further study. Although differences in breeding behavior indicate species rank, they do not necessarily warrant the recognition of higher taxonomic categories. I suggest that it is more important to emphasize the obvious close relationship of *Philohela* and *Scolopax* by combining both into a single genus than to emphasize differences associated with reproductive behavior by maintaining *Philohela* as a monotypic genus.

6) *Calidris* is used to include *Crocethia*, *Ereunetes*, and *Erolia* (cf. British Ornithologists' Union, 1952; Kozlova, 1962; Holmes and Pitelka, 1964).

7) I accept the merging of *Steganopus* and *Lo-bipes* with *Phalaropus*, long advocated by most European workers.

8) *Orthorhamphus* is considered congeneric with *Esacus*. There has been little agreement on the number of valid burhinid genera. Hartert (1924: 262) lumped *Orthorhamphus* with *Esacus*. Meinertzhagen (1924) went farther, lumping these genera and *Oedienemus* with *Burhinus*. Baker (1929: 80) accepted the lumping of *Oedienemus* and *Burhinus*, but stated that "as *Orthorhamphus* [sic] differs from *Esacus* quite as much as *Burhinus* does from that genus, it seems only consistent to have three genera, the alternative being to lump all the species in one genus." Peters (1934) followed Baker and retained three genera. Mayr (1938: 15), however, not only found the differences between *Orthorhamphus* and *Esacus* slight, but he also stated that "the two species are so similar that one is strongly tempted to unite them into one." Deignan (1945: 129) formally adopted this view, which Mayr (1949: 30), in turn, supported. This view may be correct, but to my knowledge no evidence supporting conspecificity has been presented.

Although the specific status of these forms is

unresolved, it is evident that these long-billed burhinids form a morphological unit that is distinct from the shorter-billed forms now grouped in *Burhinus*. I consider the Burhinidae to comprise two genera, *Burhinus* and *Esacus*, and *Esacus* to comprise two species *recurvirostris* and *magnirostris*.

In the following discussion the number of specimens of each species examined is given in parentheses; species for which only descriptions or photographs were available are indicated by an asterisk.

Family JACANIDAE

Microparra: *capensis*

Actophilornis: *africana* (1), *albinucha* (1)

Irediparra: *gallinacea**

Hydrophasianus: *chirurgus**

Metopidius: *indicus**

Jacana: *spinosa* (1)

Chicks of all species of jacanas are white ventrally, yellowish-brown to chestnut dorsally. There is a distinct dorsal pattern (Fig. 2A). A brownish crown patch is bordered posteriorly and laterally by black postocular stripes that meet on the occiput and extend down the neck as a thin black line. In *Irediparra* (Fig. 26), *Jacana*, and both species of



Fig. 3. *Actophilornis africana* and *A. albinucha*.

Actophilornis (Fig. 3) the stripe continues anteriorly and forms a thin central stripe on the hind portion of the crown; in *A. africana* and *Irediparra*, but not in *A. albinucha*, there is an indistinct black supraorbital spot. A broad, brownish midback stripe is flanked by narrower whitish stripes which, in turn, are bordered by brownish stripes on the sides of the body; these lateral stripes are usually paler than the midback stripe. In *A. africana*, *Irediparra*, and *Jacana* the whitish stripes are outlined by a narrow black edging, but in *A. albinucha*, and possibly in *Metopidius*, the uppermost black edging is lacking. In the species examined the wings are brownish with a black stripe on the leading edge; there is also a thin dark line along the lateral surface of the thigh.

Family ROSTRATULIDAE

*Rostratula benghalensis**

*Nycticryphes semicollaris**

I have not been able to examine chicks of either species of painted snipe, but K. A. Hindwood has provided me with several excellent photographs (Fig. 26) from which I have diagrammed the dorsal pattern of *Rostratula* (Fig. 2B). Hindwood (1960: 68-69) described *Rostratula* chicks as follows:

General colour of upperparts, including crown, light fawn; underparts slightly darker. A black stripe from the base of the upper mandible extends over the centre of the crown, where it opens out into an elongate-oval, to close again on the nape; the colour between the oval on the crown is light brown. A bright tan stripe, approximately 1/8 inch wide, extends along the entire back, and is bordered by narrower black lines. A narrow black stripe commences at the base of the lower mandible and extends through the eye along the entire length of the body about level with the small, undeveloped wings. A shorter black line, about half the length of the body, occurs on the sides of the abdomen below the wings.

The young of *Nycticryphes*, judged by a very rough sketch (Pereyra, 1943: 180) are similar to those of *Rostratula*, but may have a solid crown cap.

Family HAEMATOPODIDAE

Haematopus ostralegus (1), *palliatu*s (10), *bachmani* (2), *leucopodus**, *fuliginosus**, *ater* (1)

Oystercatchers constitute a particularly well-defined wader group, but species within the group are not easily delimited. Four to nine species have been recognized (cf. Peters, 1934; Webster, 1943; Oliver, 1955). Here I follow the American Ornithologists' Union (1957) for the American forms, Peters for the others.

Webster (1943) has previously reviewed the



Fig. 4. *Haematopus palliatus* and *H. bachmani*.

downy plumages of oystercatchers. Nearly all of the forms that he studied were individually recognizable. Yet, a constant pattern, which he described as follows (pp. 40-41), occurs throughout the family.

(1) Pure white down is present on more or less of the underparts in every form but *fuliginosus* [*bachmani* and some chicks of *H. p. frazari*].

(2) Black down forms two parallel stripes on the back, a stripe at the top of the thigh, a dot on the lores, and a dot behind the eye; also spots and a median stripe on the pileum in some forms.

(3) Some shade of drab down covers those areas of the upper parts which are not black, the throat, and (in the dark-bellied forms) most of the ventral surface.

(4) Some of the drab down of the upperparts is tipped with a shade of buff.

The pattern of *H. palliatus* diagrammed in Figure 2C may be compared with photographs of *H. palliatus* and *H. bachmani* (Fig. 4). In both species there is a definite band of dark down on the occiput and nape.

Family CHARADRIIDAE

Subfamily VANELLINAE

Vanellus vanellus (6), *crassirostris*, *armatus**, *spinus* (1), *duvaucelii* (1), *tectus* (2), *malabaricus*, *albiceps*, *lugubris**, *melanopterus**, *coronatus**, *senegallus**, *melanocephalus*, *superciliosus*, *gregarius**, *leucurus*, *cayanus*, *chilensis*



Fig. 5. *Vanellus chilensis*, *V. duraucelii*, and *V. tectus*.

(2), *resplendens*, *cinereus**, *indicus**, *macrop-
terus*, *tricolor* (1), *miles* (1)

There would appear to be relatively little variation in color or pattern of lapwing young. Typically, chicks are grayish-brown mottled with fine black markings dorsally, except for a white band on the nape (Fig. 2D). In all species but *gregarius* the mottling on the head is sharply demarcated posteriorly by a solid black band from the posterior corner of the eye, or in some cases from the auricular region, to the occiput. A black band of variable prominence extends from the hip to the tail. Most species lack a definite back pattern, but black down forms an interrupted V in *duraucelii* and *tectus*, a solid midback stripe in *spinus*, and a "broken black line down the center" in *coronatus* (van Someren 1956: 125). The venter is white in all species; *vanellus*, *chilensis*, and *indicus* possess a black pectoral band.

Chicks of *chilensis*, *tectus*, and *duraucelii* are shown in Figure 5.

Subfamily CHARADRIINAE

Charadrius: *hiaticula* (31), *semipalmatus* (37), *pla-*

cidus, *dubius* (5), *wilsonia* (9), *vociferus* (33), *melodus* (10), *thoracicus*, *pecuarius* (3), *sanctae-helenae*, *tricoloris* (1), *alexandrinus* (20), *marginatus*, *peronii* (2), *venustus**, *collaris*, *bicinctus**, *falklandicus* (1), *mongolus**, *leschenaultii**, *asiaticus**, *veredus*, *modestus**, *montanus* (10), *melanops* (1), *cinctus*, *rubricollis*, *novaeseelandiae**

This arrangement of plover species follows Bock (1958), except that *semipalmatus*, *sanctae-helenae*, *marginatus*, and *veredus* are considered full species (see Vaurie, 1964).

The basic downy pattern in *Charadrius* (Fig. 2E), like that of *Vanellus*, consists of a mottled crown patch separated from a similarly mottled back by a white or whitish nape band; this pattern is characteristic of *wilsonia* (Fig. 7), *melodus*, *pecuarius* (Fig. 6), *alexandrinus* (Fig. 6), *peronii* (Fig. 6), *venustus*, *mongolus*, and *montanus* (Fig. 6); in *modestus* (Fig. 26) and *falklandicus* (Fig. 7) the nape is pale rufous. Within this group the ground color of the dorsal down varies from whitish to orange-buff to grayish brown. In the darker forms there is a tendency for dark bands to occur on the rump (*wilsonia*, *falk-*

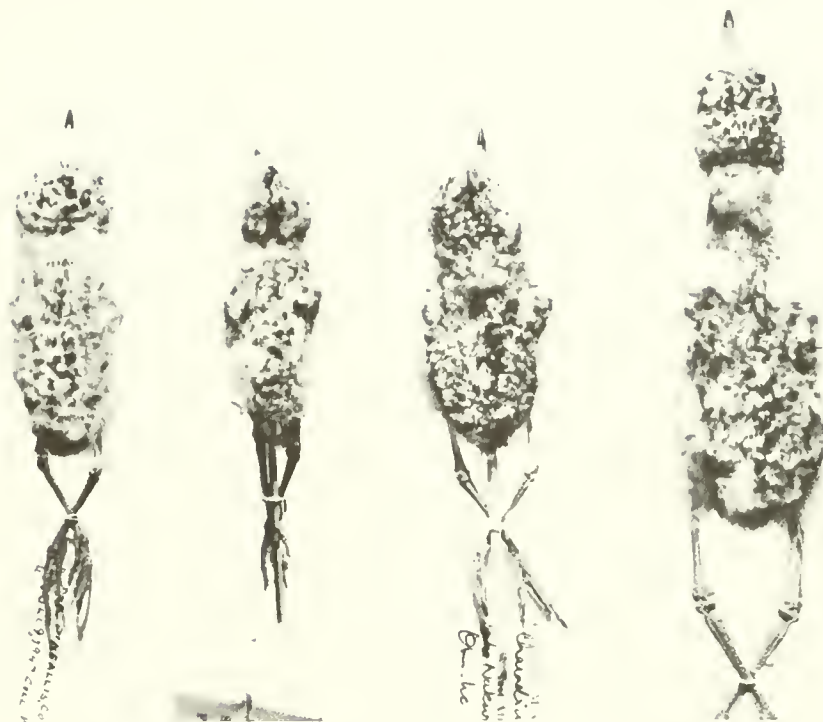


Fig. 6. *Charadrius alexandrinus*, *C. peronii*, *C. pecuarius*, and *C. montanus*.

lundicus), occiput (*wilsonia*), wing (*peronii*, *alexandrinus*), or midcrown (*peronii*, and perhaps *novaeseelandiae*); in *pecuarius* there is a narrow, interrupted V-shaped figure on the back.

Within *Charadrius*, however, the variations superimposed on the basic pattern are somewhat greater than in other wader genera. In *hiaticula* and *semipalmatus* (Fig. 7) a conspicuous black band borders the nape band; in addition, two dark bands are present on the wing, and another extends from the hip to the tail. *C. dubius* is similarly patterned, but in this species the entire crown patch is outlined in black. In *melanops* and *rociiferus* (Fig. 7) the crown patch is also encircled by black down; in addition, there is a black midback stripe, a dark band from the hip to the tail, a bold ulnar stripe, and a black pectoral band. *Charadrius tricoloris* and *C. leschenaultii* are most similar to *melanops* and *rociiferus* but lack a black anterior border to the crown patch and possess a short, black midcrown stripe; *leschenaultii* lacks a pectoral band. Two indistinct pectoral bands have been reported in *falklandicus*.

In two species, *bicinctus* and *novaeseelandiae*, the nape is lightly mottled and does not sharply separate the head from the back markings.

*Anarhynchus: frontalis**

The chick of the Wrybill Plover is "pale grey speckled with black above, white below" (Oliver, 1955: 268); it apparently lacks a distinct dorsal pattern.

Plegornis: mitchelli (1)

According to Johnson (1965: 331), the *Plegornis* chick is "uniform grey on the head and back with dove-grey throat, breast and ventral surface." In the specimen that I examined the dorsal down is brownish-gray mottled with black, the individual feathers being virtually identical to those of *Charadrius semipalmatus*; the venter is grayish-white. There is no dorsal pattern.

Pluvialis: apricaria (9), *dominica* (9), *squatarola* (11), *obscura**

Chicks of *Pluvialis*, except *obscura*, are easily distinguished from all other plover chicks by their general yellowish dorsal coloration. In *P. d. dominica* (Fig. 8), the dorsum, except for the nape, is irregularly mottled with fine black markings. An inconspicuous black midline on the forehead diverges and encircles the crown patch as an interrupted line; a broken black line from the base of the bill passes dorsal to the eye and then to the auriculars, where it joins a black malar stripe; between the eye line and the crown patch is a broad, white, supraorbital stripe that extends onto the nape. The nape is

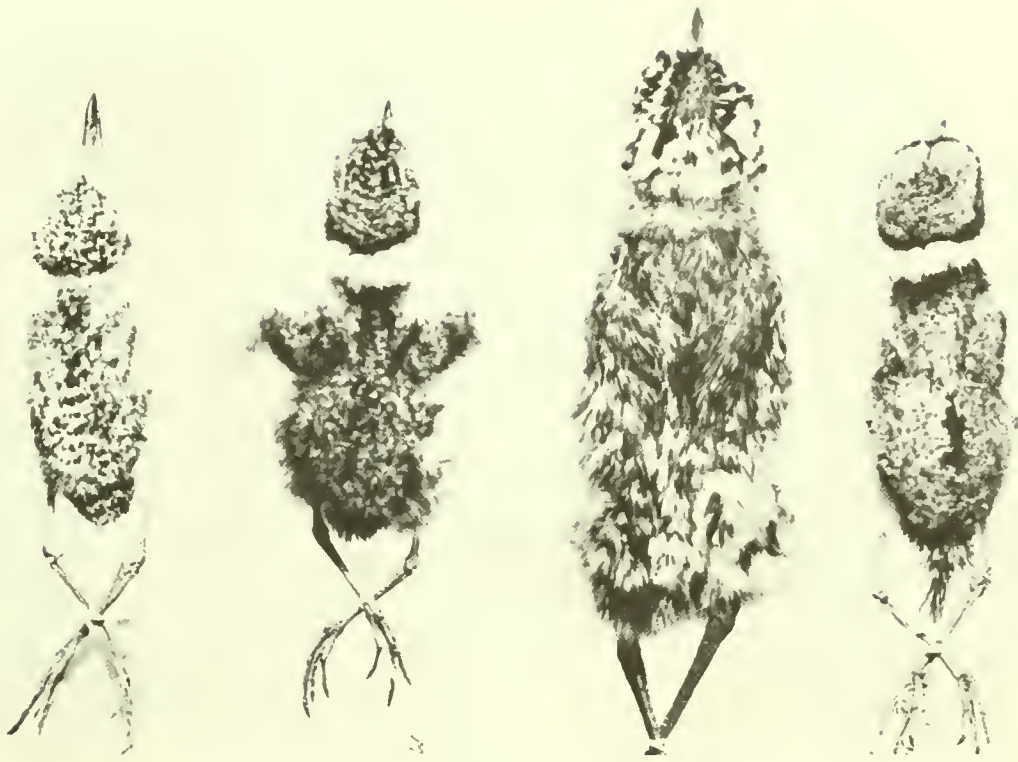


Fig. 7. *Charadrius wilsonia*, *C. semipalmatus*, *C. falklandicus*, and *C. vociferus*.



Fig. 8. *Pluvialis dominica*, *P. squatarola*, *Eudromias morinellus*, and *Oreopholus ruficollis*.

usually entirely whitish or pale yellowish, but in some chicks it is interrupted by a blackish middorsal mottling. On most chicks of this form the back is uniformly mottled, but in about 15 per cent of the chicks examined in life two whitish stripes occur on the sides of the lower back (see Fig. 2F). Vague black markings from the top of the thigh to the tail are present in some specimens. The wings are mottled proximally, white distally; black lines parallel both the radius and ulna. The venter is grayish-white. *Pluvialis d. fulva* apparently lacks the whitish nape band of *dominica* (Witherby et al., 1940: 376; Oliver, 1955: 255-256; Gabrielson and Lincoln, 1959: 329). One chick from Nome, Alaska, assigned to *fulva* (AMNH no. 751849) has a white collar, but birds from this region may be intergrades between *fulva* and *dominica* (Gabrielson and Lincoln, 1959).

The pattern in the other species of *Pluvialis* is like that of *dominica*, except that in *squatarola* (Fig. 8) the collar is broader and is never interrupted, and in *apricaria* and *obscura* the collar is absent.

Eudromias: morinellus (4)

Witherby et al. (1940: 388) described the Dotterel chick (Fig. 8) as follows:

Down on fore-head white or light buff with a median black line extending from base of bill to crown; crown ochraceous-buff and white irregularly marked black; on hinder crown a crescent-shaped patch of white, below which a black semi-circular line extends below eye from lores to lores; nape white intermixed with dusky; remaining upper-parts sandy to ochraceous-buff irregularly mottled black and greyish-white; superciliary stripe, ear-coverts and cheeks white; a narrow blackish line extends from lores through eye to nape; remaining under-parts greyish-white, down dusky at base, breast suffused cream.

The darker down on the lower back forms a band on the midline that is bordered laterally by two indistinct whitish lines.

Oreopholus: ruficollis (1)

Chicks of this species (Fig. 8) are complexly colored. The forehead, lores, sides of head, and nape are whitish, lightly flecked with tan and dark brown. The venter is buffy. There is a thin brown line from the base of the bill to the anterior corner of the eye and, in addition, there is a thin brown malar stripe. No very definite dorsal pattern can be detected; a whitish nape separates the crown cap from the similarly colored back, and an indistinct brown central stripe on the lower back is flanked by light buffy stripes.

Pluvianellus: socialis

Young of this species are unknown.

Family SCOLOPACIDAE

Subfamily TRINGINAE

Prosobonia: cancellatus (including *parvirostris*; see Greenway, 1958: 260), *leucoptera*

Prosobonia leucoptera once occurred on Tahiti and Eimeo in the Society Islands, but it is now extinct and known only from the type specimen; its young were never described. *Prosobonia cancellatus* occurs on "small, isolated islands situated on fringing reefs of atolls in Tuamotu (Paumotu or Low) Archipelago" (Greenway, 1958: 260); its young are unknown.

Bartramia: longicauda (9)

The Upland Plover chick (Fig. 9) is distinct from chicks of all other species of the Scolopacidae. Its brown and tan dorsal down is tipped with extensive buffy or whitish edges, resulting in a generally "scaly" appearance. I can recognize no regular arrangement to the back markings, but those on the head form a definite pattern: a faint dark stripe extends from the base of the bill to the forehead, where it broadens into an indefinite crown patch that is irregularly flecked with lighter markings; prominent postocular stripes parallel the border of the crown patch and nearly join on the occiput; there is a large dark spot below the eye and another on the nape. The venter is whitish, tinged with buff on the neck and chest.

*Numenius: minutus**, *borealis*, *phaeopus* (16), *tahitiensis* (1), *tenuirostris*, *arquata* (8), *madagascariensis*, *americanus* (12)

Descriptions exist for chicks of only five of the eight curlew species. Allen and Kyllingstad (1949) have described the color and pattern for four species and have diagrammed the dorsal pattern in *phaeopus* and *tahitiensis*. To their account I can only add that the pattern of the *minutus* chick does not differ appreciably from that of *phaeopus*, as far as can be determined from Turgarinow's (1929) and Vorobiev's (1963) illustrations.

In all species the ground color of the down is tan or grayish. The venter is unpatterned, but the down on the upper chest is usually more intensely colored than that on the neck or belly. The dorsum is marked with dark brown or blackish in a pattern that appears to be nearly constant in all species. The pattern, shown for *phaeopus* (Figs. 2G, 9) is characterized by a light-centered crown patch, a bifurcation of the dark middorsal stripe in the shoulder region, and a diamond-shaped figure on the lower back. In many individuals of *phaeopus* a well-marked postocular stripe parallels the crown



Fig. 9. *Bartramia longicauda*, *Numenius phaeopus*, and *Limosa haemastica*.

patch and extends onto the occiput. There are additional black markings on the shoulders and wings and lateral to the "diamond"; dark stripes from the hip lead to the tail.

The only variation from this pattern occurs in *N. americanus*, in which the borders of the crown patch are mottled, not solid (see illustration in Bent, 1929: Pl. 20).

Limosa: *limosa* (7), *haemastica* (13), *lapponica* (4), *fedoa* (6)

The pattern of downy godwits (Fig. 2H) is similar to that of curlews. It differs in having the crown patch solid, and the middorsal stripe, which is continuous with the "diamond" on the lower back, fails to bifurcate at the shoulder. As in the curlews, there are additional dark areas on the wings and back, and a line from the top of the thigh runs toward the tail.

There is little variation in the basic pattern. In a few specimens of *haemastica* (Fig. 9) there is a second, smaller "diamond" on the rump. In all species except *lapponica* there is a prominent dark spot in the temporal region; in *haemastica* this mark is usually continuous with the crown patch.

Chicks of *limosa*, *lapponica*, and *fedoa* are similar in color, the ground color of the down being light buffy brown; chicks of *haemastica* are much

gray and the dorsal markings are nearly black.

Tringa: *erythropus* (10), *totanus* (15), *stagnatalis* (1), *nebularia* (7), *guttifer**, *melanoleuca* (1), *flavipes* (18), *ocrophus* (6), *solitaria* (1), *glareola* (10)

In this list of species I have placed *flavipes* next to *melanoleuca*. Nichols' (1923) arguments that these species are not closely related and that *melanoleuca* is a mimic of *flavipes*, which may have been the basis for Peters' separation, are unconvincing. I have arbitrarily placed "*Pseudototanus*" *guttifer* next to *nebularia*.

The genus *Tringa* comprises two groups, the "shanks" (*erythropus* through *flavipes*) and the "wood sandpipers" (*ocrophus*, *solitaria*, *glareola*), that are accorded generic status by the A. O. U. (1957). If formal taxonomic recognition of these groups is deemed necessary, I would prefer to recognize them as the subgenera *Totanus* and *Tringa*, respectively.

Chicks of the Nearctic species of the "shanks" (*melanoleuca*, *flavipes*; Figs. 10, 26) are grayish with black markings dorsally, white ventrally; chicks of the Old World species average browner dorsally, but there is some overlap in coloration. The dorsal pattern (Fig. 2I) consists of: 1) a solid crown patch, 2) three dark lines on the back that



Fig. 10. *Tringa flavipes*, *T. melanoleuca*, *T. erythropus*, and *T. solitaria*.

may converge at the rump, and 3) dark lines from the hip to the tail that usually merge with the lateral stripes on the back. There are small dark patches on the wings and, in most individuals, on the lateral surface of the thigh. A dark line from the base of the bill to the anterior corner of the eye is present in all forms, and in all but *nebularia* there is a prominent postorbital stripe that may extend to the occiput.

Pattern variation is somewhat greater in *Tringa*, even within some species, than in most other

genera. Some of the variations in head pattern are diagrammed in Figure 11. Variation in back pattern usually involves changes in the width or prominence of the stripes, but the lateral stripes may be interrupted, and in one specimen of *T. totanus* (UMMZ no. 64773) the middorsal stripe is broadened to a diamond with a light central area.

Chicks of the "wood sandpipers" do not differ greatly in pattern from those of the "shanks," although the ground color of their dorsal down averages warmer brown. The middorsal stripe

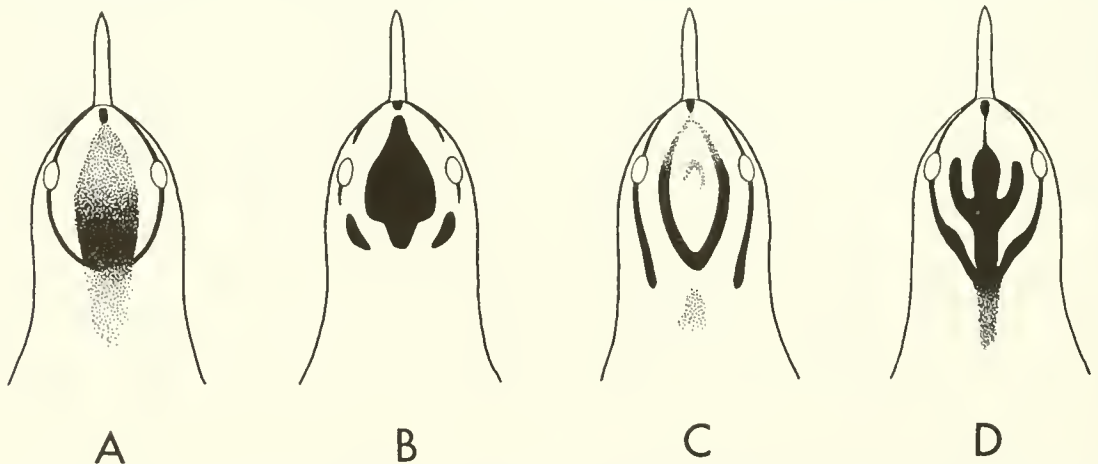


Fig. 11. Variation in the head patterns of tringine sandpipers: A. *T. erythropus*; B. *T. melanoleuca*; C. *T. totanus*; and D. *T. ocropus*.



Fig. 12. *Xenus cinereus*, *Actitis macularia*, and *Heteroscelus incanus*.

continues onto the nape and is usually continuous with the posterior border of the crown patch. In *glareola* and *ocrophus* a stripe from the base of the bill passes through the eye and ends on the occiput; in *solitaria* (Fig. 10) the preorbital portion of the stripe is absent and the postorbital portion is reduced to a small spot above the auriculars.

Xenus: cinereus (1)

Xenus chicks (Fig. 12) are light gray-brown with dark markings dorsally, whitish ventrally; the down on the neck and chest may be tipped with buff. The pattern (Fig. 2J) is like that of *Tringa* but the dark dorsal markings have been reduced, the crown patch to a single stripe from the base of the bill to the occiput, the three back stripes to a prominent middorsal line and two indistinct lateral lines; the lines from hip to rump are similarly reduced and prominent markings on the wings and thighs are lacking. As in *Tringa* there is a well-marked line through the eye.

Actitis: hypoleucos (5), *macularia* (25)

In *Actitis* the pattern is simple (Fig. 2K) and consists only of a single blackish middorsal stripe

from the base of the bill to the rump; a conspicuous stripe from the base of the bill passes through the eye to the occiput. Chicks of both species are whitish below; dorsally those of *hypoleucos* tend to be buffy brown, those of *macularia* (Fig. 12) pale grayish, but there is some overlap.

Catoptrophorus: semipalmatus (3)

The ground color of Willet chicks varies from light grayish to buffy brown; the dark brown or blackish pattern is typical of *Tringa*.

*Heteroscelus: brevipes**, *incanus* (6)

Tattler chicks (Fig. 12) are gray to bluish-gray above, white below; there is usually a faint tinge of gray on the throat and chest. Chicks that I have examined are nearly void of dorsal markings and have only a narrow transverse band of darker down on the rump. However, in Shortt's (1947) illustration of *incanus* a faint central stripe is shown on both the back and head, and one of the chicks photographed by Weeden (1965) appears to have a crown stripe. Chicks of *incanus* have a well-marked line from the base of the bill to the anterior corner of the eye; in one specimen the line extends slightly



Fig. 13. *Aphriza virgata*, *Arenaria interpres*, and *Arenaria melanocephala*.

posterior to the eye; chicks of *brevipes* are apparently identical to those of *incanus*, except that the eye stripe may be even more conspicuous.

Subfamily ARENARIINAE

Aphriza: virgata (1)

I have examined only one partly-grown chick of this species (Fig. 13), but an excellent photograph of newly hatched chicks has recently been published (Wetmore, 1965: 324). Both in color and pattern these chicks are nearly identical to those of *Calidris canutus*. The calidridine pattern is described below.

Arenaria: interpres (9), *melanocephala* (6)

Turnstone chicks are colored like those of *Tringa totanus*. Ridgway (1919: 51) described chicks of *A. interpres* (Fig. 13) as: "Above light drab to drab-gray, irregularly mottled or marbled with black; forehead buffy drab-gray, with a median elongated black spot or irregular streak; a distinct loreal streak of black, from bill to eye [which continues to the temporal region]; under parts dull white, the chest shaded with brownish gray." Chicks of *A. melanocephala* (Fig. 13) are similar, perhaps averaging slightly grayer.

Except for the forehead stripe and the eye-line, there is no consistent pattern in this genus. Some

chicks have two narrow, indistinct, parallel lines in the shoulder region and a mounted specimen in the Royal Ontario Museum (no. 35618) shows the typical three-striped back pattern of *Tringa*.

Subfamily SCOLOPACINAE

Chicks of the Scolopacinae (except *Scolopax*) and of the Calidridinae possess an unusual type of down, sometimes called "bottle-brush" feathers (Fig. 14). Barbs of these feathers are intertwined for most of their length, forming a rather rigid structure. From their tips short, white, densely packed barbules radiate and interlock with similar barbules of adjacent barbs, thus forming the (usually) white puffs of dorsal down that characterize the downy plumage of most members of these subfamilies. Long, sparse, dark barbules originate laterally from the basal three-quarters of each barb. This portion of the feather corresponds to the dark "patterned" areas on other wader chicks. Therefore, the arrangement of the white dotting reflects a definite underlying pattern. In interpreting the pattern diagrams for *Gallinago*, *Limnodromus*, and *Calidris* one must recall that the areas diagrammed as dark will appear whitish on the specimens.

Limnodromus: griseus (13), *scolopaceus* (3), *semi-*

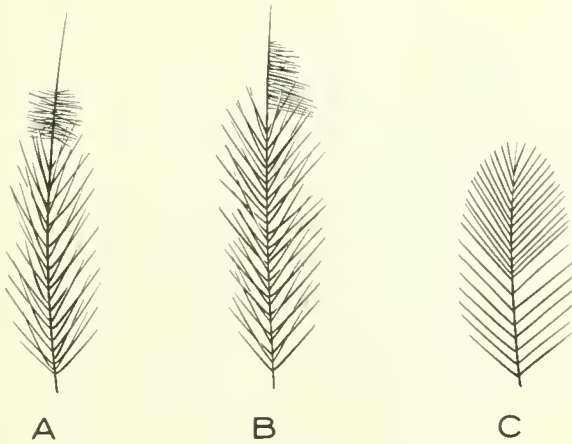


Fig. 14. Structural differences in the superficially similar white-tipped dorsal down of: A. *Calidris alpina*; B. *Thinocorus rumicivorus*; C. *Cursorius temminckii*. For each species a single barb is illustrated.

*palmatus**

The ground color of dowitcher chicks varies from light golden brown (*griseus*; Fig. 15) to dark chocolate brown (*scolopaceus* and *semipalmatus*). Bottle-brush feathers are confined to the back and outline a definite pattern (Fig. 2L), which consists of paired lines on the midback flanked by lines of

variable prominence on the sides of the body; short lines extend from the hip toward the tail. On the head, the crown patch is solid and is separated from the eye by a broad, whitish, supraorbital stripe; a continuous line extends from the base of the bill to the crown patch; malar stripes and dark throat patches are absent, although a small interramal spot may be present in a few individuals of *griseus*.

Coenocorypha aucklandica (1)

The single chick that I have examined is in such poor condition that little can be made of the pattern. A stripe from the base of the bill extends to the anterior canthus; another runs up the forehead and onto the crown, but its posterior limit cannot be determined. The chick is uniformly grayish brown above and below and is similar to chicks of *Gallinago paraguaiæ*. Bottle-brush feathers are present but inconspicuous, and dark throat markings are absent.

Gallinago (= *Capella*; see Mayr 1963: 402): *solitaria*, *hardwickii* (1), *nemoricola*, *stenura*, *megala**, *nigripennis* (1), *macroductyla* (1), *media**, *gallinago* (including *delicata*, 9), *paraguaiæ* (1), *nobilis* (1), *undulata*, *stricklandii* (1), *jamesoni**, *imperialis*



Fig. 15. *Limnodromus griseus* and *Gallinago gallinago* (dorsal and ventral).



Fig. 16. *Gallinago nobilis*, *G. stricklandii*, and *G. hardwickii*.

The linear placement of *stricklandii* and *imperialis* follows De Schauensee (1966: 98).

Snipe chicks are not well represented in collections and several species are undescribed. The species that I have examined are similar in color and pattern. Extensive dark brown or black markings on a (usually) chocolate ground color are found in most species, but in *paraguaiiae* the black markings are virtually absent, and in *hardwickii* and *stricklandii* (Fig. 16) the ground color is grayish or light tan. In all species a prominent black spot at the base of the upper mandible is separated from the crown cap by a light-colored transverse stripe from lore to lore; all species possess a malar stripe, which may be interrupted, and all but *jamesoni* show dark patches of variable prominence on the throat (Fig. 15); a small interramal spot is present in some species.

The dorsal pattern of *G. gallinago* is shown in Figure 2M. There appears to be no regularity to the complex crown markings; the back pattern is like that of *Limnodromus*. Bottle-brush feathers occur in all snipe, being abundant in some (e.g., *gallinago*, Fig. 15), virtually absent in others (e.g., *paraguaiiae* and *hardwickii*).

De Schauensee (1966: 97) considered *G. paraguaiiae* (in part) conspecific with *G. gallinago* but raised *G. p. audina* to species rank. I have not been

able to examine a chick of *G. paraguaiiae* (sensu De Schauensee), but Meinertzhagen (1926: 509) states that young of *G. p. brasiliensis* closely resemble those of *G. g. gallinago*. Young of *G. p. audina* differ markedly from those of *G. gallinago* and presumably from those of other races of *G. paraguaiiae* sensu Peters (1934); this supports De Schauensee's interpretations. De Schauensee (1966: 98) also suggested that *G. jamesoni* should be merged with *G. stricklandii*, but chicks of these forms differ slightly; in *jamesoni* throat patches are absent, whereas in *stricklandii* they are large and prominent.

*Lymnocyptes: minima**

Jack Snipe chicks are nearly identical to those of *Gallinago gallinago*, but possess "a conspicuous and well-defined inframandibular bar of white" (Lowe, 1934: 44).

Scolopax: rusticola (5), *mira* (see Vaurie, 1965), *saturata*, *celebensis*, *rochussenii*, *minor* (12)

Only two species of woodcocks could be examined (Fig. 17); their back patterns are identical but the head markings of *rusticola* are less extensive than those diagrammed for *minor* (Fig. 2N). Presumably chicks of other species are similar; if variation exists it would most likely occur in *rochussenii*, the adults of which differ in pattern from other wood-



Fig. 17. *Scolopax minor*, and *S. rusticola*.

cock species.

Young woodcocks are tan with dark brown markings. A solid crown cap extends from the base of the bill to the nape, where it broadens into a large dark patch. Three stripes on the back extend from the shoulder region to the tail, the central stripe being much broader than the lateral ones. There is a large dark area on the lateral surface of the thigh, and several small dark areas occur on the wings. The venter is unpatterned, but the neck and chest are more heavily tinged with brown than is the abdomen. Unlike young snipe there are no dark markings on the throat and bottle-brush feathers are not present.

Subfamily CALIDRIDINAE
(= EROLIINAE of Peters, 1934)

Calidris: *canutus* (3), *tenuirostris**, *alba* (1), *pusilla* (40), *mauri* (6), *ruficollis**, *minuta* (1), *temminckii* (2), *subminuta*, *minutilla* (21), *fuscicollis* (4), *bairdii* (23), *melanotos* (6), *acuminata**, *maritima* (3), *ptilocnemis* (13), *alpina* (22), *ferruginea** (= *testacea*)

Eurynorhynchus: *pygmeus* (4)

Limicola: *falcinellus* (6)

Micropalama: *himantopus* (74)

Tryngites: *subruficollis* (1)

Philomachus: *pugnax* (3)

Downy young of the six genera listed here (Figs. 18, 19) are so similar in pattern that they are most conveniently discussed together. This pat-

tern, which is more easily diagrammed than described (Fig. 20) basically consists of irregular dark brown markings on the head and an "hour-glass" shaped figure on the back. As in the snipe, it is the bottle-brush feathers that give the clue to the pattern. The back pattern is not apparent in all chicks, although it is evident in *C. ptilocnemis* and *M. himantopus* (Figs. 18, 19). This may be due to the make of the skin, the age of the chick, or individual variation, but the age of the chick seems to be the most important variable. In older chicks the white barbs at the tips of the bottle-brush feathers are worn off or disentangled; thus, the barbs separate and the pattern becomes diffused.

In spite of their great similarity, two groups of calidridine chicks can be recognized. In the first (*pusilla*, *mauri*, *ruficollis*, *minuta*, *temminckii*, *minutilla*, *fuscicollis*, *melanotos*, *acuminata*, *ptilocnemis*, *alpina*, *ferruginea*, *pygmeus*, *falcinellus*, *himantopus*, *pugnax*), the ground color of the dorsal down is yellowish to chocolate brown; a relatively distinct dark crown patch is bordered by broad, whitish, supraorbital stripes that extend to the occiput; face markings are variable, but are usually not pronounced; all species have a varying amount of brownish wash on the neck and chest. In the second group (*tenuirostris*, *canutus*, *alba*, *bairdii*, *maritima*, *subruficollis*), the ground color of the dorsal down is brownish-gray and the dark markings are more extensive; the crown is interrupted by numerous white flecks and no definite cap is present; distinct supraorbital lines are absent; dark face markings are common and more intricate than in the first group; all are whitish ventrally.

Family RECURVIROSTRIDAE
Subfamily IBIDORHYNCHINAE

Ibidorhyncha: *struthersii**

Ibisbill chicks are brownish-gray dorsally, pure white ventrally. Down on the nape is slightly paler than that on the back. The only evidence of dorsal pattern is an indistinct band of darker down that crosses the rump. A line from the base of the bill passes through the eye to the temporal region.

Subfamily RECURVIROSTRINAE
Himantopus: *himantopus* (7)

Chicks of *H. h. mexicanus*, the only race that I have examined, are grayish above, white below. The most conspicuous features of the dorsal pattern (Fig. 2P) are the two dark lines that extend from the shoulder region toward the rump; in some

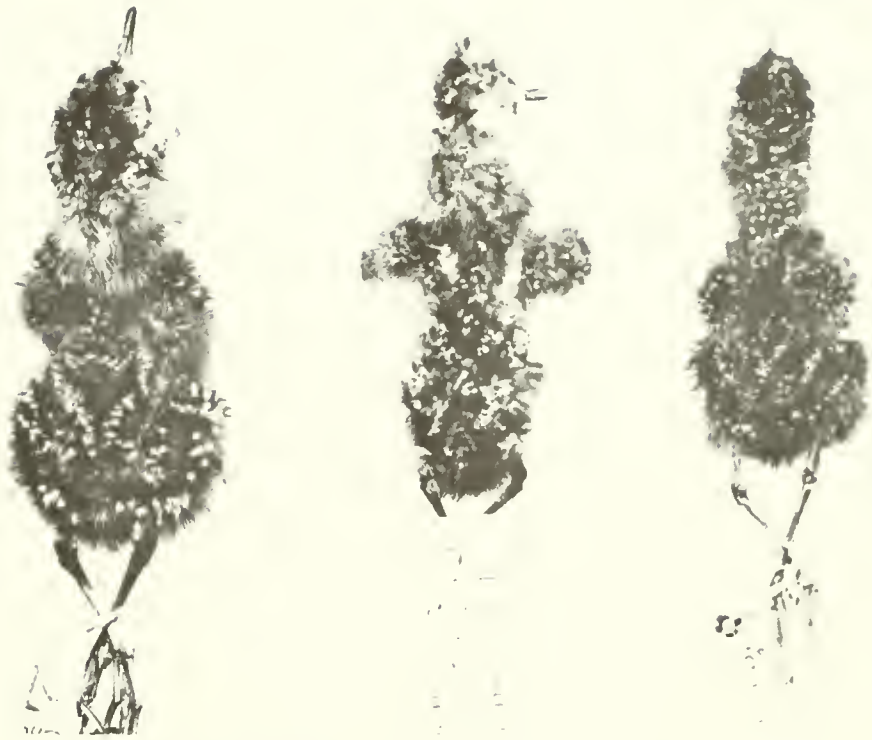


Fig. 18. *Calidris ptilocnemis*, *Eurynorhynchus pygmeus*, and *Limicola falcinellus*.



Fig. 19. *Micropalama himantopus*, *Tryngites subruficollis*, and *Philomachus pugnax*.

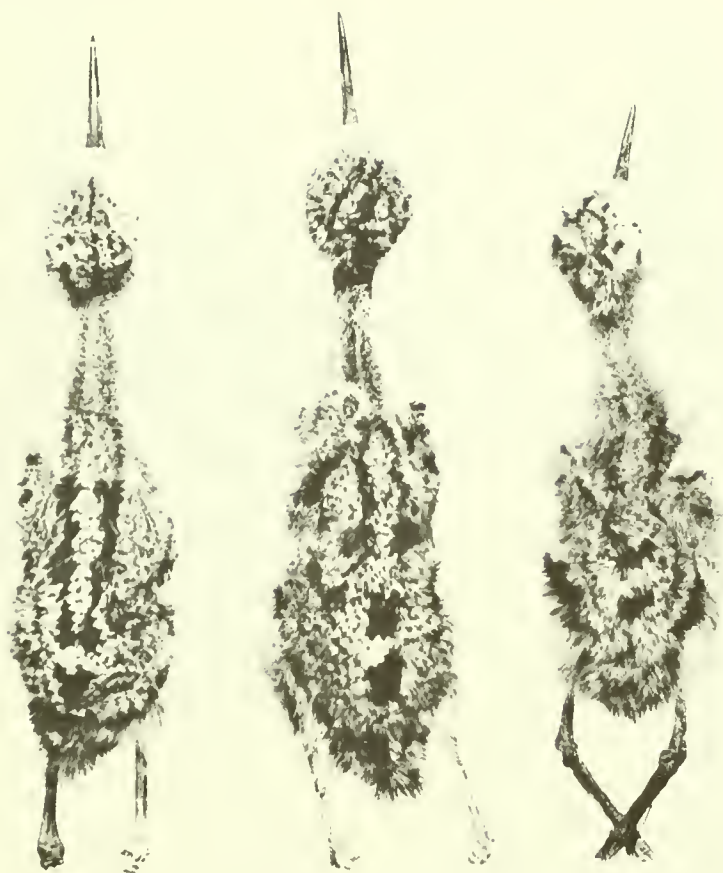


Fig. 20: *Himantopus himantopus* (two left), and *Recurvirostra americana*.

specimens these fuse on the midback and continue posteriorly as a single stripe; in others they extend to the rump before joining (see Fig. 20). Lines from each hip meet at the rump. A small spot occurs on the lateral surface of the thigh and a stripe on the wing parallels the radius. Head markings are variable; the crown and occiput are irregularly spotted; in all specimens there is a thin line from the crown to the nape, and in some there is an indistinct transverse band on the occiput. All chicks have a small spot at the anterior corner of the eye; the postorbital area is usually unmarked except for a spot at the temporal canthus, but one specimen has a well-marked postorbital stripe that reaches the occiput. The nape is pale gray and is not mottled.

The pattern in most other races of *himantopus* is apparently like that of *mexicanus*. However, Housse (1945: 131) reported that young of *melanurus* have a black pectoral band. Chicks of *novaezealandiae* are "covered with a dark brown down" (Oliver, 1955: 304).

*Cladorhynchus: leucocephala**

According to Glauert and Jenkins (1931: 3), chicks of the Banded Stilt are "covered with whitish down black at the base." These authors did not note any dorsal pattern, and G. M. Storr, who reexamined two nestlings preserved in fluid, confirmed (pers. comm.) the lack of obvious pattern.

Recurvirostra: avosetta (4), *americana* (17), *novae-hollandiae**, *andina**

Avocet chicks (Fig. 20) are light tan with dark markings dorsally, white ventrally. Their dorsal pattern is like that of *Himantopus*, though less conspicuous. However, in avocets, the paired lines on the back always fuse at midback, never at the rump; in addition, a stripe from the base of the bill passes across the eye to the occiput.

Family PHALAROPODIDAE

Phalaropus: tricolor (6), *lobatus* (17), *fulicarius* (11)

Phalarope chicks (Fig. 21) are yellowish with black markings dorsally, yellowish on the throat and neck, whitish on the belly. The ground color of the dorsal down varies; it is buff in *tricolor*, golden

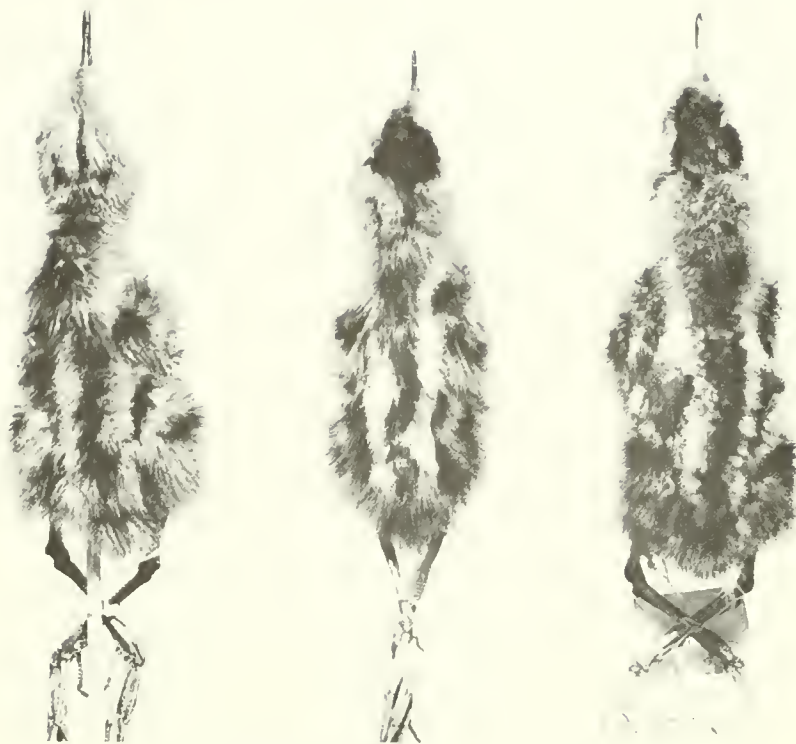


Fig. 21. *Phalaropus tricolor*, *P. lobatus*, and *P. fulicarius*.

yellow to light brown in *lobipes*, and light or dark brown in *fulicarius*. The dorsal pattern is similar in all species. In *lobipes* (Fig. 2Q), for example, there is a dark crown patch, three stripes lead from the shoulder region to the rump, and a stripe extends from the hip toward the tail. All individuals possess a small postorbital spot; some have a thin line from the base of the bill to the anterior corner of the eye.

There is little pattern variation in this genus, although the prominence of the dorsal striping varies in *lobipes* and *fulicarius*, some individuals appearing almost black. All individuals of *fulicarius* show an eye-stripe and a postorbital spot; these facial markings are absent in *tricolor*. The crown patch in *tricolor* is reduced to a thin central stripe that adjoins a narrow band on the occiput, thereby forming an anchor-shaped marking.

Family DROMADIDAE

*Dromas: ardeola**

Sharpe (1896: 29) described the young of the Crab-Plover as "covered with ashy-grey down above, slightly mottled with dusky; cheeks and under surface of body dingy grey, the general appearance of the bird being uniform."

Family BURHINIDAE

Burhinus: oedinemus (5), *senegallus**, *vermiculatus**, *capensis**, *bistriatus**, *superciliaris*, *magnirostris* (4)

Esacus: recurvirostris (1), *magnirostris*

Burhinus and *Esacus* chicks (Fig. 22) are grayish brown on the back and chest and dirty white on the throat and belly. The dorsal pattern (Fig. 2R) consists of two dark lines running nearly in parallel from the shoulder to the rump; a dark line from the hip extends toward the tail. There is an irregular dark patch on the forehead and scattered dark markings occur on the crown and occiput. Post-ocular stripes extend onto the occiput and continue down the neck; in some species these appear to be continuous with the paired back stripes. A prominent malar stripe leads from the base of the bill to the auriculars.

Family GLAREOLIDAE

Subfamily CURSORIINAE

Pluvianus: aegypticus (1)

The color pattern of the Egyptian Plover chick (Fig. 23) is plover-like. A broad, white nape band surrounded by black stripes that diverge from the posterior corner of the eye separates the lightly mottled, sand-colored back from the similarly colored crown. The venter is white, as are the wings, except for a narrow sandy stripe on the leading

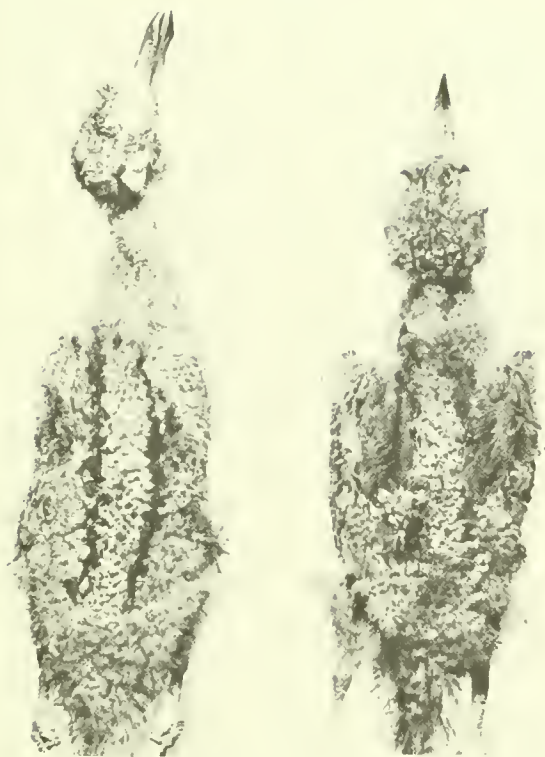


Fig. 22. *Burhinus oedicnemus*, and *Esacus recurvirostris*.

edge.

Cursorius: *cursor* (1), *coromandelicus**, *temminckii* (2)

Young of *Cursorius temminckii* (Fig. 23) have the "upper parts mottled black, buff, and red-brown. The nape is crossed by a buff-white band. On the underparts chin and throat whitish, dull reddish brown on the breast" (Stejneger, 1965: 32). Chicks of

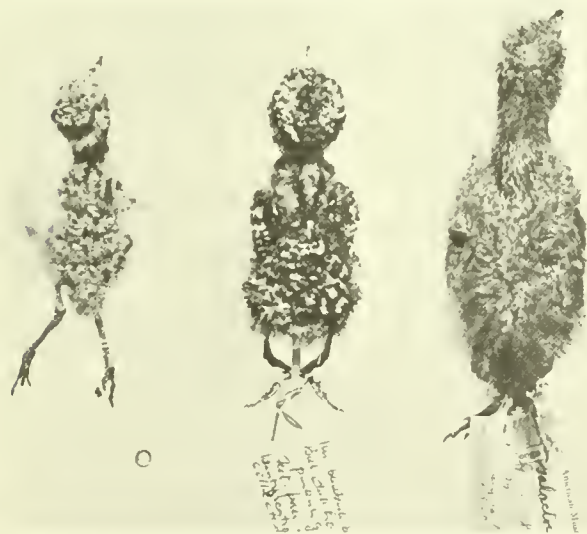


Fig. 23. *Pluvianus aegypticus*, *Cursorius temminckii*, and *Glaucola nuchalis*.

coromandelicus appear to be virtually identical to those of *temminckii*, but may lack a white nape (Ticehurst, 1926: 376). *Cursorius cursor* chicks are patterned like those of *temminckii*, but are paler.

Cursorius chicks appear to be covered with short, flat, contour feathers, but on close inspection it is evident that the "rachis" of each "contour feather" is but a single barb, and that each down feather contains six to eight such barbs. Barbules originating from the barbs are stiff, closely packed, and lie in a single plane. Because of their structure, they do not merge with barbules of adjacent barbs and, thus, each unit looks and functions like an independent contour feather (Fig. 14).



Fig. 24. *Peltohyas australis*.

Rhinoptilus: *africanus**, *cinctus*, *chalcopterus**, *bi-torquatus*

I know of no descriptions for young of *Rhinoptilus*, but a chick of *R. africanus* (Fig. 26) photographed by G. L. Maclean is much like that of *Cursorius temminckii*. It is reddish brown with patches of white and black scattered on the dorsum in no definite pattern; a fine black stripe extends from the base of the bill to the anterior corner of the eye; the venter appears reddish-brown but the color is not clearly visible in the photograph. Unlike *C. temminckii*, this species does not possess a white nape band. The curious flattened feathers noted in *Cursorius* also occur in *R. africanus*.



Fig. 25. *Attagis gayi*, *A. malouinus*, *Thinocorus orbignyianus*, and *T. rumicivorus*.

The chick of *Rhinoptilus chalcopterus* photographed by Steyn (1966: 242) appears to be much more similar to chicks of *Charadrius* or *Vanellus* than to young of *R. africanus*. Its dorsum appears uniformly colored, except for a broad, white, nape band that is bordered anteriorly by a black stripe. Unfortunately, neither the head pattern nor the feather structure are visible in Steyn's photograph. *Peltohyas: australis**

Chicks of this species (Fig. 24) are similar in color, pattern, and feather structure to those of *Cursorius* and *Rhinoptilus africanus* (description, in litt., and photographs by K. A. Hindwood). *Peltohyas* lacks a white nape band and is uniformly buffy on the venter.

Subfamily GLAREOLINAE

*Stiltia: isabella**

Glareola: pratincola (1), *maladivaram**, *nordmanni*, *ocularis*, *nuchalis* (1), *lactea**, *cinerea**

Pratincole chicks are brownish-gray, indistinctly mottled with dark brown dorsally, pale brown or dirty white ventrally. There is no definite dorsal pattern. Apparently, most species have a fine line from the base of the bill to the eye. In *G. nuchalis* (Fig. 23) the line continues from the posterior corner of the eye to the occiput, where it meets a midcrown stripe; both of these markings are indistinct. A midcrown stripe is also present in *G.*

pratincola and in *Stiltia* (Chaffer, 1949: Pl. 2).

Family THINOCORIDAE

Attagis: gayi (1), *malouinus* (1)

Thinocorus: orbignyianus (1), *rumicivorus* (1)

In *Attagis* the buff or grayish-brown dorsal down is boldly crossed by wide dark markings that occur in no obvious pattern. The venter is uniformly grayish-brown in *gayi*, whitish with a buff tinge on the throat in *malouinus*.

Chicks of *Thinocorus* are whitish ventrally, gray-brown flecked with whitish dorsally. In *T. orbignyianus* dark brown markings form a midcrown line and two short supraorbital lines, whereas in *T. rumicivorus* (Figs. 25, 26) the dark head markings are less distinct, and prominent white supraorbital lines are present. In each species there is a large dark V-shaped figure on the back, which in *rumicivorus* is bordered laterally by a broad band of white-tipped feathers; in the single specimen of *orbignyianus* available this whitish band was either reduced or obscured by the make of the skin. In both species, but particularly in *rumicivorus*, white-tipped feathers are scattered over much of the dorsum. Although these feathers, at first glance, are reminiscent of "bottle-brush" feathers, their structure is quite different (Fig. 14). In this case the whitish, distal barbules are concentrated on one side of the barb, and tend to spiral along the

barb; in lateral view they look like wind-pruned spruce trees, with all the branches emanating from the leeward side. Seed-snipе chicks are shown in Figure 25.

Family CHIONIDIDAE

Chionis: alba (3), *minor* (1)

Jones (1963: 67) described the young of *C. alba* as

"clothed in a dark brown down which bears light-colored, hairlike tips and therefore presents a 'smutty brown' appearance." The natal down is followed by a second, dark gray down. The chick of *C. minor* is like that of *alba*, though perhaps slightly grayer; however, I have not been able to compare the chicks directly. There is no evidence of a distinct dorsal pattern in either species.

RELATIONSHIPS IN THE CHARADRII

In the following discussion relationships indicated by chick color patterns are compared with present interpretations of shorebird inter-relationships. In making these comparisons I have, unfortunately, been unable to consider fully the findings of Kozlova (1962) and Yudin (1965), because translation of their works were unavailable. Where relationships indicated by downy plumages correspond to current views I have assumed that these are well founded; where they do not correspond, or where an alternative relationship is indicated, I have attempted to re-evaluate the evidence on which current views are based and to employ additional evidence in determining affinities.

Within some families (e.g., Jacanidae, Haematopodidae) chick patterns are nearly uniform; this precludes their use in suggesting relationships below the family level. The uniformity does confirm that species assigned to such families are correctly placed, but, more interestingly, it suggests that the patterns characterizing these groups may have remained essentially unchanged throughout much of the group's history. In other families (e.g., Scolopacidae) there is sufficient variation that infrafamilial relationships can be postulated. Often the pattern characterizing one genus can be easily transformed into that of another, which I regard as evidence of close affinity; in some cases the reasons for pattern change can be inferred. Where I have outlined possible pattern transformations, no phylogenetic implications are intended by the order of transformation given; the reverse transformation is equally possible.

JACANIDAE, ROSTRATULIDAE

The relative constancy of chick patterns in the Jacanidae precludes their use in clarifying inter-generic relationships. However, jacana plumages are so similar to those of young painted snipe that

common ancestry may be postulated. Conceivably these resemblances might be convergent and indicate no more than similar selection for bold, disruptive patterns in wet tropical regions. However, there are several reasons for rejecting convergence. 1) Nests are usually placed in different habitats, those of the jacanas on floating vegetation, those of painted snipe in wet, grassy fields. Presumably, chicks are likely to be encountered near the nest; if so, it is hard to imagine a common background toward which the convergence might be directed. 2) The chick patterns in these families are distinctive and are unlike those of any other waders. Moreover, the patterns are complex, which minimizes the chance of independent origin and subsequent convergence. 3) The patterns of one family can easily be transformed into that of the other; by extending the postorbital stripes of the jacanas onto the back and adding a light center to the crown, and by losing a lateral stripe, a painted snipe pattern can be formed.

The idea of relationship between these families is not new. It has been proposed by Furbringer (1888) and Beddard (1901). It is difficult to understand why Lowe (1931a) did not group these families together, since all but one of the osteological characters he presented for *Rostratula* are applicable to the Jacanidae. (The exception is the claimed presence of supraoccipital foramina in *Rostratula benghalensis*. I have not seen a skull of this species, but supraoccipital foramina are not present in the skull illustrated by Yudin (1965: 82), nor are they present in the one skull of *Nycticryphes* that I have examined.) Surprisingly, Lowe failed to note the similarity of the chicks.

In groups as distinct as the Jacanidae and Rostratulidae, it is difficult to provide evidence that would prove close relationship. However, all the available evidence supports this idea and I know of none that contradicts it. I would place both families

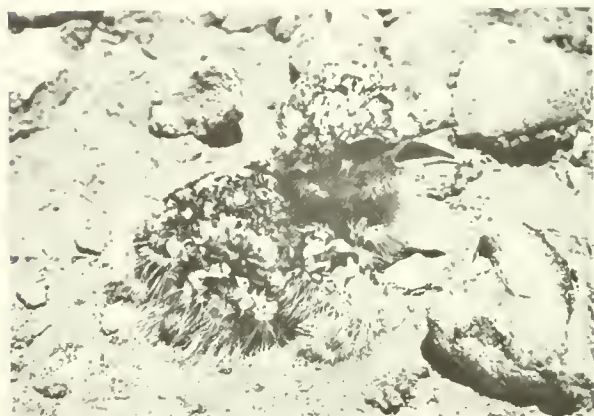


Fig. 26. Left to right, top to bottom. Chicks of *Irediparra gallinacea* (Jacanidae): photo by Peter Roberts; *Rostratula benghalensis* (Rostratulidae): photo by K. A. Hindwood; *Charadrius modestus* (Charadriidae): photo by Gordon Maclean; *Rhinoptilus africanus* (Glareolidae): photo by Gordon Maclean; *Tringa flavipes* (Scolopacidae); *Thinocorus rumicivorus* (Thinocoridae): photo by Gordon Maclean.

in a single superfamily, Jacanoidea.

DROMADIDAE

This monotypic family is restricted to the Indian Ocean region. According to Lowe (1931b), its affinities are with the Glareolidae and Chionididae, but most other workers (e.g., Peters, 1934; Mayr and Amadon, 1951; Wetmore, 1960; Storer, 1960) place it near the Burhinidae. The similarity of adult Crab-Plovers in body form to the burhinids and in plumage pattern to the recurvirostrids might indicate that they are distantly related to that major wader line (see below). However, the young are unpatterned and cannot be used to support any relationship. Therefore, I retain the Crab-Plover in a monotypic superfamily, Dromadoidea.

This species' unpatterned young are unusual, but its nesting habits and unpatterned eggs are unique in the Charadrii. Crab-Plovers nest in underground burrows; their chicks are apparently nidicolous and are fed in the burrows by the parents (Lowe, 1916b: 319; Archer and Godman, 1937: 497). Ticehurst (1923: 72) suggested that the absence of chick patterning in this species represented the retention of an ancestral condition, but this position seems untenable. Patterned chicks are of almost universal occurrence in the Charadrii, and in those few cases in which pattern is absent it can be most reasonably postulated that the loss is secondary.

There are two possible hypotheses to explain pattern loss in the Crab-Plover. In nearly all hole-nesting species, the eggs and young are whitish and unpatterned; pattern loss in the Crab-Plover may represent a parallel response. On the other hand, since ancestors of the Crab-Plover were almost certainly surface-nesters with patterned eggs (a patterned egg has been reported: Anon., 1921: 21-22) and young, it is possible that pattern was lost in response to selection for uniform coloration on a uniformly sandy substrate, and that burrow nesting evolved later. The fact that Crab-Plover young are countershaded (i.e., darker above than below), a condition that is presumably of value above ground, may support the latter interpretation. If pattern was lost subsequent to burrow-nesting, and if young remain in the burrows until the down feathers are replaced, it is curious that countershading has been retained.

Lowe (1916b: 319-320) suggested that burrow nesting in Crab-Plovers may have evolved in response to predation on the eggs. However, I would suggest that this behavior may be an extreme condition derived from the habit of burying the

eggs, ostensibly to protect them from intense solar radiation during the parents' inattentive periods. This function has been attributed to several species, including *Charadrius alexandrius* and *C. pecuarius* (Blaker, 1966: 100). Excessive heating may be a major cause of embryo mortality in desert birds (Maclean, 1967: 564).

HAEMATOPODIDAE, RECURVIROSTRIDAE, BURHINIDAE

Intrafamilial Relationships

Within the Haematopodidae and Burhinidae the chick patterns are too uniform to indicate intrafamilial relationships. In chicks of some melanistic oystercatchers (e.g., *H. bachmani*, *H. o. unicolor*) the normal, disruptive pattern is obscured by the darkened ground color of the dorsal down, but this doubtless reflects an over-riding secondary selection for cryptic coloration on dark nesting substrates, not common ancestry.

In the Recurvirostridae the patterns confirm the obvious close relationship of *Himantopus* and *Recurvirostra*. *Cladorhynchus* is similar to these genera and is intermediate in the characters that have been used to separate them (Ridgway, 1919: 436; Mathews, 1913-1914: 153); however, its chicks are pale and unpatterned. Since *Cladorhynchus* nests on the shores of salt lakes (Serventy and Whittell, 1951: 158), where the substrate coloration may be unusually light, it seems reasonable to postulate that pattern and color have been lost secondarily as a means of enhancing cryptic coloration.

Relationships within *Himantopus* and *Recurvirostra* cannot be inferred from the chicks, but variation in the chicks of *H. himantopus* is greater than in any other species examined; this might indicate that more than one species of stilt should be recognized. The "absence" of pattern in *H. h. novaezealandiae* may be an artifact of description, since the pattern could be obfuscated by the dark down. On the other hand, the presence of a pectoral band in young of *H. h. melanurus*, if Housse (1945) is correct, represents a decided departure from the usual pattern that deserves further investigation.

Interfamilial Relationships

The "two-lined" dorsal patterns in the Haematopodidae, Recurvirostridae, and Burhinidae are extremely similar. The patterns are simple and could have arisen independently, but the families utilize such varied nesting habitats (e.g., rocky beaches, sandy beaches, dry grasslands, wet mar-

shes) that the independent evolution of similar disruptive patterns for a common background seems unlikely. Furthermore, close relationship between the Haematopodidae and Recurvirostridae is supported by osteological (Lowe, 1931b) and protein (Sibley, pers. comm.) evidence. Conder (1964: 77) has noted behavioral similarities between these families, and Maclean (1966: 168) has pointed out that the curious "legs out" resting posture of these families is also shared by the Burhinidae.

The Burhinidae were placed by Lowe (1931a) and Yudin (1965) nearest the Otididae (Gruiformes), but charadriine affinities are indicated by protein evidence (Sibley, 1960) as well as by chick plumages; thick-knee chicks differ markedly from those of bustards. The structure and patterning of individual midback feathers in the young of most species of Haematopodidae, Recurvirostridae, and Burhinidae are similar, being short, flattened, and crossed by a dark bar of variable prominence. The possible taxonomic significance of these feathers remains to be determined, for in species that nest in cooler or wetter areas the down is long and fluffy, and the barring is either reduced or obscured by the changed feather structure.

Peters (1934), without explanation, placed the Ibisbill (*Ibidorhyncha*) in the Recurvirostridae. Other workers have placed it with the oystercatchers (Seeböhm, 1887), near the oystercatchers (Hartert, 1912-1921; von Boetticher, 1934), in the Vanellinae (includes also *Himantopus* and *Recurvirostra*; Baker, 1929), and as a monotypic subfamily of the Charadriidae (Lowe, 1931b). Dresser (1907) remarked on its behavioral similarities to lapwings in defense of its nest. Although the Ibisbill's affinities are to this broad group of waders, I know of no evidence that would unquestionably link it more closely to the Recurvirostridae than to any of the other families mentioned. The dark, unpatterned chicks are of no aid. Again, the loss of pattern is probably secondary, but in this case the correlation is with the streamside shingle flats on which the species nests. The advantage of uniformly colored chicks in this habitat is shown by Ludlow and Kinnear's (1934) photograph of a crouching chick. Until a conclusive study of Ibisbill relationships is made, it should be placed in a monotypic family.

I include the Haematopodidae, Recurvirostridae, Ibidorhynchidae, and Burhinidae in the Charadrioidae.

CHARADRIIDAE VANELLINAE

Too few downy lapwings are available to test the possible taxonomic value of their plumage patterns. The patterns of most species are quite similar and the slight variations that occur (e.g., the presence of a black pectoral band in at least three species) seem to be taxonomically unimportant. Young of *Vanellus*, however, are so similar to young *Charadrius* that common ancestry for these genera is confirmed.

CHARADRIINAE

The several variations of chick patterns in *Charadrius* seem to reflect color and type of nesting substrates and thus are not useful in showing species relationships within this genus. For example, chicks of species that nest on light-colored beaches (e.g., *alexandrinus*, *melodus*) are pale and lack conspicuous dark markings, whereas chicks of species that nest on darker and more irregularly-colored substrates (*semipalmatus*, *dubius*, *vociferus*) are darker and may be more boldly marked. These apparent correlations should be considered only tentative until detailed knowledge of the nesting ecology of all species is available. The absence of a white nape band in chicks of *bicinctus* and *novaeseelandiae* might also reflect similar nesting habitats; in any event, there is no reason to assume it indicates close relationship. The presence or absence of a black pectoral band, as in the lapwings, also seems to be of no taxonomic importance (see below).

As noted earlier, similarities between the plumage patterns of adults and downy young are far more pronounced in *Charadrius* than in any other wader genus. The reason for this similarity can only be inferred. However, most members of this genus characteristically nest on open beaches or in other areas of sparse vegetation. Thus, the chicks, like the adults, cannot usually escape predators by hiding amid vegetation but must rely on their disruptive plumage patterns. It is interesting that with one exception chicks of species in which the adults are unbanded or possess only one dark pectoral band have no breast band; in *melanops* both adults and young have a single band. On the other hand, young of the two-banded plovers *vociferus* and *tricoloris* have a single breast band and young of *falklandicus* have two indistinct bands; young of *bicinctus*, however, are unbanded.

Huxley (1958: 98-99) suggested that the presence

of a double breast band in adult *vociferus* might be a function of size. However, this suggestion does not hold for all species of *Charadrius* in which the adults are two-banded, nor is there any correlation between size of chicks and the presence or absence of a breast band. If size alone were important, one might expect to find breast bands in chicks of most lapwings. Since breast bands presumably act to supplement the general disruptive effect of the plumage pattern, they may be of greatest selective value in particular habitats. Further speculation on their significance in chicks must await detailed analyses of the nesting habitats of all species as well as studies of the functional significance of breast bands in adult birds at all seasons.

Bock (1958: 52-53) found that variations in plumage patterns of adult *Charadrius* plovers were probably of little taxonomic importance. Because of the similarity between adult and chick patterns, the chick patterns must also be considered unreliable indices to relationships within this genus.

The chick of *Anarhynchus*, though lacking a white nape, is like those of several species of *Charadrius*, a genus to which it is very closely allied (Bock, 1958). The relationships of *Phegornis* have

long been in question; some workers have included it with the plovers, others with the sandpipers. Yet, its chicks, although also lacking a white band on the nape, are charadriine, and other characters confirm that *Phegornis* is a plover (Zusi and Jehl, in prep.). The loss of the nape band would seem to be correlated with this species' apparent preference for nesting on sand and shingle flats bordering mountain streams (Johnson, 1965: 329-330; cf. *Ibidorhyncha*, *Heteroscelus*).

The affinities of *Pluvianellus* are unknown. This species has been considered a plover (Peters, 1934), perhaps allied to the *Charadrius* group (Bock, 1958: 79-80), but adults bear some resemblance to turnstones (*Arenaria*), and perhaps its affinities are to that genus. Unfortunately, its chicks are unknown. Pending further study this form is best retained in the Charadriidae.

Patterns in *Pluvialis* young are like those of *Charadrius*, differing only in minor details of face pattern, in the presence of supraorbital stripe, and, in some individuals of *P. dominica* at least, in having faint whitish lines on the lower back. All these characteristics are present in *Eudromias* and, in a veiled condition, in *Oreopholus*. The

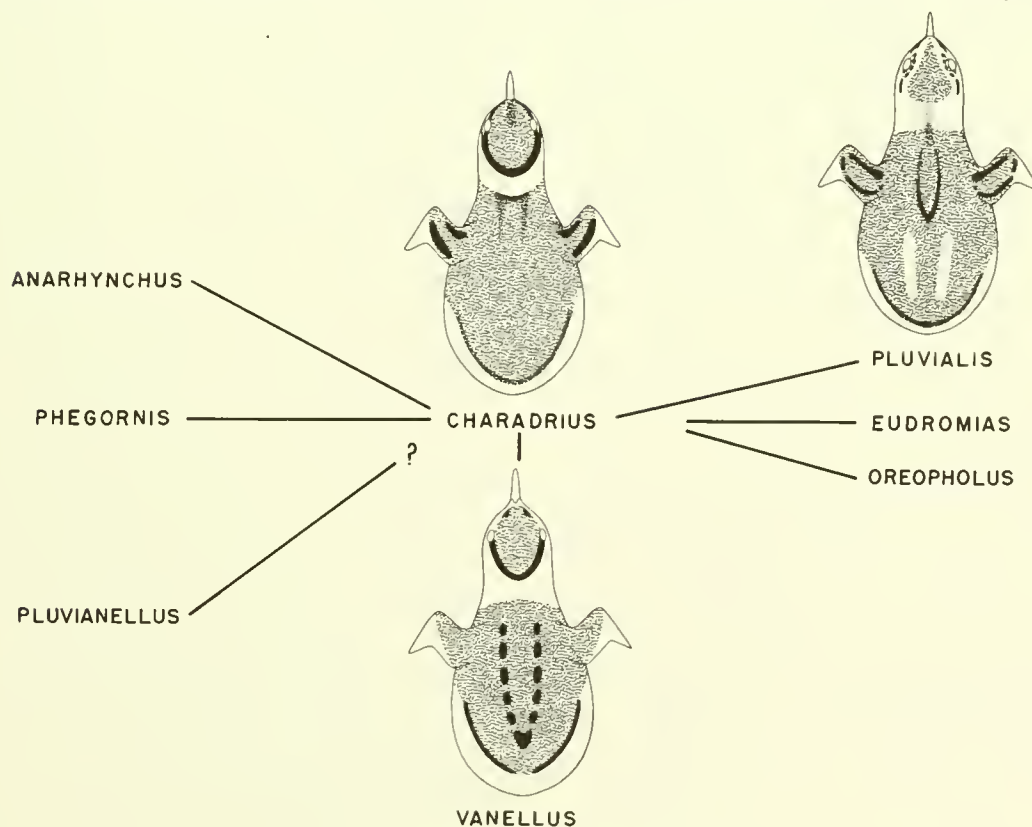


Fig. 27. Phenetic relationships of genera in the Charadriidae indicated by the patterns of the downy young.

similarity in back color between chicks of *Pluvialis*, *Eudromias*, and *Oreopholus* (golden to light brown) may indicate relationship; more certainly it reflects selection for cryptic coloration on tundra and moorland. Lowe (1915: 339) interpreted the downy plumage of *Oreopholus* as that of an "aberrant Dunlin" (*Calidris alpina*), but he was misled by the white-tipped down feathers that contrast with the brownish back, resulting in a somewhat calidridine-like appearance.

The close relationship of *Charadrius*, *Pluvialis*, *Eudromias*, and *Oreopholus* has been previously advanced; the B.O.U. (1952) merged the first three genera, and Bock (1958) the latter two. However, I fail to see any advantage to such widespread lumping without first understanding relationships among these genera. I would suggest that *Pluvialis* represents a relatively recent radiation of *Charadrius* in (mainly) arctic regions; the origins of *Eudromias* and *Oreopholus* are far less certain. Pending further study I retain all four as distinct genera.

Chick plumages do not clarify relationships within *Pluvialis*. Chicks of both *apricaria* and apparently *P. d. fulva* lack the prominent white collar of *squatarola* and usually *P. d. dominica*. The significance of this difference is unknown, but it is interesting that development of the white collar apparently increases latitudinally, being absent in *apricaria*, variable in *dominica*, and prominent in *squatarola*. If this correlation is accurate, the latitudinal variation might reflect the decreasing height of vegetation northward. If chicks of northern species or populations occur frequently in exposed situations, selection would favor the retention, or development, of a disruptive marking. Precise data on the physiography of habitats used by each species and on possible geographic variation in collar markings in *P. dominica* are needed to test this suggestion.

According to Bock (1958: 87-88), *P. obscura* probably "descended from a group of some species of *Pluvialis* that remained in New Zealand to breed." Of the two migrant congeners that occur in New Zealand, *squatarola* and *dominica*, the former is very rare (Oliver, 1955: 254). Whether the absence of a white collar in chicks of *obscura* and in *P. d. fulva*, the race of the Golden Plover that winters in New Zealand, indicates common ancestry or a parallel response to similar nesting habitats is unknown.

A tentative outline of generic relationships in the Charadriidae is outlined in Figure 27.

Interfamilial Relationships

Plovers are closely allied to the Haemotopodidae-Recurvirostridae groups (Lowe, 1931b: 740; Simmons, 1964: 282), most workers placing them close to the oystercatchers. Although chick patterns typical of these families seem dissimilar, it would require no great change to derive a plover pattern (mottled head and back, white nape) from that of the recurvirostrids (paired back lines, light-colored neck) or of the oystercatchers (paired back lines, dark nape). The occurrence in *Vanellus duvaucelii* of a pattern combining the white nape of the plovers with the paired back stripes of the recurvirostrids and oystercatchers suggests how the pattern transformation could have been accomplished.

On the basis of size and adult plumage patterns the lapwings would seem closer to the oystercatcher-recurvirostrid line than are the charadriine plovers.

GLAREOLIDAE

Intrafamilial Relationships

The genus *Rhinoptilus* comprises two obvious species groups, *africanus* and *cinctus*, and *chalcop-terus* and *bitorquatus*. The first of these originally constituted the genus *Hemerodromus*, which Sharpe (1893) merged with *Rhinoptilus* for unstated reasons. The difference in color patterns of the adults of these groups are as strong as between any two glareolid genera. The cryptically colored chicks of *R. africanus* differ markedly from the disruptively marked chicks of *R. chalcop-terus* both in color pattern and feather structure. The significance of these differences is unclear. Yet, the differences seem great enough to indicate that *Rhinoptilus* may not be a natural taxon.

Relationships among the glareolid genera are badly in need of review. The chick plumages suggest possible affinities between *Pluvianus*, *Rhinoptilus chalcop-terus*, and *Cursorius*, and between *Cursorius*, *Peltohyas*, and *Rhinoptilus africanus*. They are of no help in suggesting relationships between courser and pratincole genera.

Interfamilial Relationships

Lowe (1931b) considered the Glareolidae closely allied to the Chionididae and Dromadidae, but Peters (1934) placed the family in a superfamily between the Burhinoidea and Thinocoroidea. However, Bock (1964) pointed out that differences between the Glareolidae and Charadriidae are minor, and he implied that these families might be very

TABLE 1
EXTERNAL FEATURES OF CURSORIINE GENERA COMPARED WITH THOSE
OF *CHARADRIUS*. DATA AND CHARACTERS USED, IN PART, FROM BOCK, 1964.

	<i>Cursorius cursor</i>	<i>Pluvianus aegypticus</i>	<i>Rhinoptilus africanus</i> , <i>R. chalcopterus</i>	<i>Peltohyas australis</i>	<i>Charadrius wilsonia</i>
Relative length of tarsus (based on tarsus/wing ratio).	intermediate; cursoriine	short; charadriine	intermediate, long; cursoriine	short; charadriine	short; charadriine
Tarsal scutellation	rectangular; cursoriine	rectangular, subdivided on both surfaces; intermediate	rectangular; cursoriine	rectangular on anterior surface, divided on posterior; intermediate	hexagonal; charadriine
Anterior toes	flattened; cursoriine	intermediate	flattened, intermediate; cursoriine, intermediate	flattened; cursoriine	not flattened; charadriine
Middle toe	pectinate; cursoriine	not pectinate; charadriine	pectinate, weakly pectinate; cursoriine	not pectinate; charadriine	not pectinate; charadriine
Adult plumage	cursoriine	cursoriine	cursoriine	most like plovers (<i>cf.</i> <i>Eudromias</i>); charadriine	charadriine
Downy plumage	cursoriine	charadriine	cursoriine; charadriine?	cursoriine	charadriine
Tip of premaxilla	not inflated; cursoriine	not inflated; cursoriine	slightly inflated; intermediate	slightly inflated; intermediate	inflated; charadriine
Dorsal edge of mandible	decurved; cursoriine	decurved; cursoriine	decurved (slightly in <i>cinctus</i>); cursoriine	very slightly decurved; charadriine	straight; charadriine

closely related. If evidence for affinity exists, it should be found in the Cursoriinae rather than in the more specialized Glareolinae.

Bock's speculation was prompted by his study of *Peltohyas australis*, an unusual plover-like species that he reassigned to the Charadriidae on the basis of skull characters. These characters are worthy of review. Bock (1964: 402) assumed that for most of the features studied "a sharp break exists between the plover and glareolid condition." As he correctly indicated, this process is more plover-like in *Peltohyas*, but the significance of this observation is border of the palatines, the maxillopalatines, and the ectethmoid region show little variation within each family; *Peltohyas* shows the charadriine

configuration for all but the ectethmoid structure. However, other characters show more variation than he recognized. The following discussion is based on skeletal examination of the following: *Rhinoptilus africanus* - 3; *R. cinctus* - 1; *R. chalcopterus* - 2; *Peltohyas australis* - 1; *Glareola pratincola* - 1; *Vanellus* - 7 species; *Charadrius* - 15 species.

1. Articular surface of the quadrate. In the coursers *Rhinoptilus africanus* and *R. cinctus*, which Bock was unable to study, this surface is like that of the plovers and thus is not useful in familial separation.

2. Articular region of the mandible. The internal process of the articular in most coursers is unlike

that of most plovers. Yet, in both groups the structure is variable and its configuration in *Rhinoptilus africanus* and *R. cinctus* is like that of some of the smaller species of *Charadrius*. As Bock indicated, this process is more plover-like in *Peltohyas*, but the significance of this observation is uncertain. Contrary to Bock's assertion (p. 393), the occurrence of a dorsal extension on the retro-articular process does not allow the separation of the Charadriidae and Glareolidae. A small extension occurs in both *R. chalconotus* (not shown in Bock's Fig. 3; cf. Yudin, 1965: 87, Fig. 18) and *R. cinctus*; in *R. africanus* the process is well developed and is intermediate between the *Cursorius* and *Charadrius* condition. However, in *Peltohyas* the process is charadriine.

3. Configuration of the external nares. In the plovers and in *Peltohyas* the external naris terminates in a long, thin slit; in most glareolids it terminates in a blunt, rounded shape. An intermediate condition is approached in *R. cinctus*.

4. Terminal swelling of the premaxilla. The condition in *Peltohyas* is like that in *Rhinoptilus africanus* and *R. cinctus* and is not as inflated as in *Charadrius wilsonia*, for example. However, the

ramphotheca covering the premaxilla is more inflated in *Peltohyas* than in *Rhinoptilus*.

In summary, although some of the characters Bock employed to support the reallocation of *Peltohyas* are less useful than he believed, there is no doubt that the skull morphology of this species is more charadriine than cursoriine. However, I do not consider these characters, which may be merely aspects of a single character complex, sufficient to justify a reallocation. Moreover, the color pattern and feather structure of *Peltohyas* chicks is typically cursoriine and is most like that of *R. africanus*, which poses some difficulty for the acceptance of Bock's view. I retain *Peltohyas* in the Cursoriinae.

External morphology played no part in Bock's reassignment of *Peltohyas*, for the characters he studied (p. 385-387) neither supported nor rejected his conclusion. Nevertheless, it is instructive to reconsider the condition of these and other characters in all genera of the Cursoriinae and to compare them with the condition found in the plovers (Table 1). Three of the four courser genera show combinations of courser and plover characters or intermediate conditions. This finding, plus gradation in

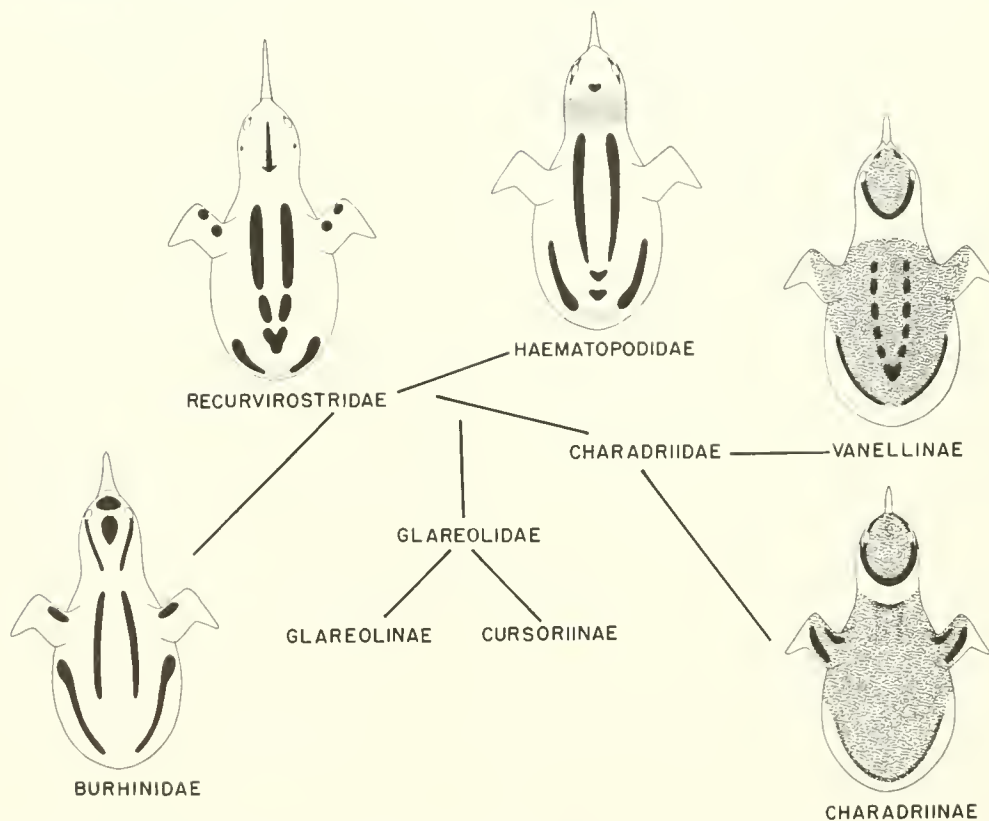


Fig. 28. Phenetic relationships in the Charadrioidae (in part) indicated by the patterns of the downy young.

skull characters, strongly indicates, as Bock suggested, that the dividing line between the Glareolidae and Charadriidae is not clear. I consider the recognition of the Glareoloidea superfluous and place the Glareolidae next to the Charadriidae in the Charadrioidea.

The relationships among the families of the Charadrioidea discussed thus far are diagrammed in Figure 28.

SCOLOPACIDAE TRINGINAE

This subfamily is most conveniently divided into three tribes, Numenini, Tringini, and Prosoboniini. The separation of the curlews and their allies has been suggested previously. Both Lowe (1931b) and Kozlova (1962) recognized this group as a distinct subfamily under the name Limosinae, although each used limits that differ from those proposed here. (Numeninae has priority over Limosinae, being the oldest family-group name for genera included in this taxon; K. C. Parkes, pers. comm.). Lowe (1927, 1931b) included *Prosobonia cancellatus* (= *Aechmorhynchus parvirostris*) in this group, but there is more evidence to link it with the Tringini (Zusi and Jehl, in prep.). Kozlova (1962) included *Limnodromus* but did not comment on the affinities of *Bartramia*.

NUMENINI.—Affinity between *Numenius* and *Limosa* has been recognized by many workers (Lowe, 1931b; Kozlova, 1962; cf. A.O.U., 1957) and is confirmed by the similarity of their chicks. By doubling the midback strip in the shoulder region, adding a light center to the crown patch, and broadening the midback stripe on the lower back, the *Limosa* pattern would be transformed into that of *Numenius*. The affinities of *Bartramia* are to the curlews (Lowe, 1931b; 758-761). However, the chick of this form is unlike that of the curlews, except for a rough similarity in crown pattern. The reason for this difference is not clear; possibly the pattern of the white-tipped back feathers in *Bartramia* is convergent to the "scaly" back pattern found in juvenile fringillids and other forms that inhabit prairies. Interestingly, chicks of *Limosa fedoa* and *Numenius americanus*, which may be sympatric with *Bartramia*, have typical godwit or curlew patterns.

TRINGINI.—Chick patterns are especially useful in suggesting interrelationships of tringine genera, for their variation is relatively large. For example, a graded series leads from the "three-striped" pattern of *Tringa* to *Xenus*, in which the lateral

stripes are reduced, to *Actitis*, which possesses only a single middorsal stripe, to *Heteroscelus*, in which the dorsal pattern is virtually absent. I do not wish to imply that this necessarily represents a phylogenetic series, for the loss of pattern in these species that tend to nest along streams or in areas of uniformly colored substrate could have occurred independently. However, morphological and behavioral similarities also indicate close affinity of *Actitis* and *Heteroscelus* (Dixon, 1933: 176-177). *Xenus*, whose chick pattern is intermediate between those of *Tringa* and *Actitis*, has similarities to both genera. Ferguson-Lees (1959: 89) described the species as an "exaggeration of the Common Sandpiper" (*A. hypoleucos*), and Neufeldt et al. (1961) thought its calls and breeding displays resembled those of *T. nebularia*. Further studies are necessary.

The chick of *Catoptrophorus* is like that of *Tringa*.

INTERTRIBAL RELATIONSHIPS.—Close relationship of the Numenini and Tringini is generally acknowledged. Their chicks differ, but merely by interrupting the lateral stripes of *Tringa* and by adding a light center to a broadened mid-back stripe the *Limosa* pattern would be attained. As noted, back patterns in *Tringa* are variable and diamond-shaped figures occasionally occur. Head patterns similar to those of *Numenius* and *Limosa* are also found among the Tringini (Fig. 11 B, C; cf. Figs. 2 G, H). I believe the Prosoboniini to be derived from the Tringini, but chicks of *Prosobonia* are not available to test this suggestion.

Relationships in the Tringinae are diagrammed in Figure 29.

ARENARIINAE

The affinities of the turnstones have always been a problem. Some workers have considered them related to the plovers, others to the sandpipers. But, whatever their familial alignment, they have almost universally been grouped in a subfamily with the Surf-bird (*Aphriza*). The great differences between the young of these genera show that the Arenariinae is not a natural taxon. *Arenaria* young are most similar to those of tringine sandpipers in which the "three-striped" pattern has been almost obliterated. *Aphriza* chicks, however, are typically calidridine. I tentatively consider turnstones to represent a plover-like radiation from the Tringinae; there is no other downy plumage in the Charadrii from which a turnstone plumage could be easily derived. For reasons discussed elsewhere

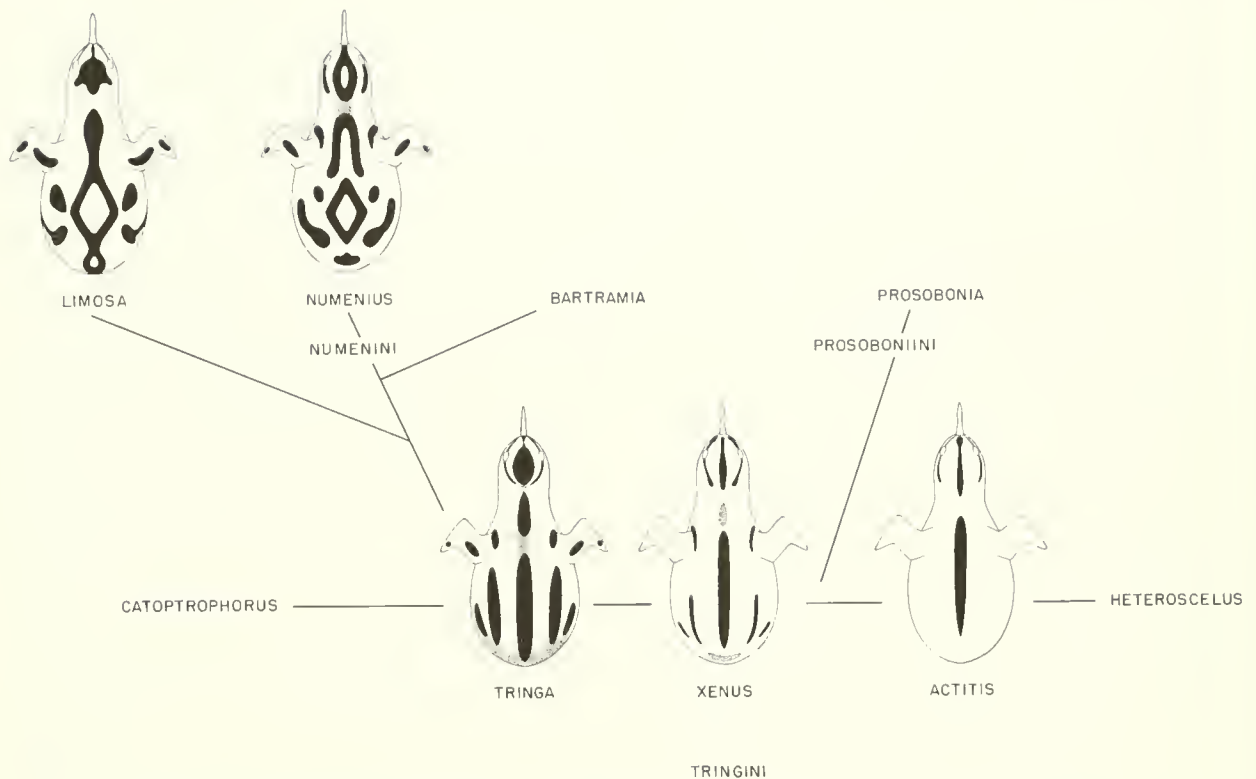


Fig. 29. Phenetic relationships of genera in the Tringinae indicated by the patterns of the downy young.

(Jehl, 1968), I place the Surfbird in the Calidridinae.

SCOLOPACINAE

The idea of close affinity between *Gallinago* and *Scolopax* is of long standing. Adults of these genera are morphologically similar and several South American species of *Gallinago* (*stricklandii*, *jamesoni*, *imperialis*) that were formerly placed in *Chubbia* (Peters, 1934) seem to bridge the gap neatly between the longer-legged, slender snipe and the squat, robust woodcocks. Yet, chicks of *Scolopax* and *Gallinago* are dissimilar. The close relationship of these genera is so widely accepted that the lack of similarity in their chicks may indicate little more than the danger of relying on too few characters in determining relationships. Since snipe tend to nest in marshy areas and woodcocks in forested regions, some differences in chick patterns might be predicted. However, in view of the similarity of downy patterns within other wader subfamilies, it is somewhat disturbing to find that nowhere among the snipe and their allies are there downy patterns that even vaguely approximate that of *Scolopax*, and, furthermore, that the variation in snipe and woodcock downy plumage is insufficient to give any clues to how one

plumage pattern could have been evolved from the other. This transformation is far more difficult to achieve than reference to the pattern diagrams might suggest, for it requires extensive changes in color and feather structure as well as in pattern (cf. Figs. 2 M, N; 16, 17). On the other hand, it requires little imagination to visualize the evolution of a *Scolopax* pattern from that of a tringine sandpiper.

Although *Scolopax* and *Gallinago* can be presumed to have arisen from a common ancestor, which may have been tringine, the great differences between their chicks suggest that these genera are more distantly related than is currently recognized. Pending a re-examination of these relationships I suggest that a separate subfamily, Gallinagoninae, be established for the snipe and their allies. This separation has also been suggested by Verheyen (1958a) on the basis of osteological characters as well as chick plumages.

The chicks of species formerly assigned to *Chubbia* are typically snipelike. I interpret the similarities between the adults and *Scolopax* as convergent. These woodcock-like snipe occur only in South America, where the most extensive snipe radiation has taken place; woodcocks, in spite of their otherwise widespread distribution, are absent from that continent.

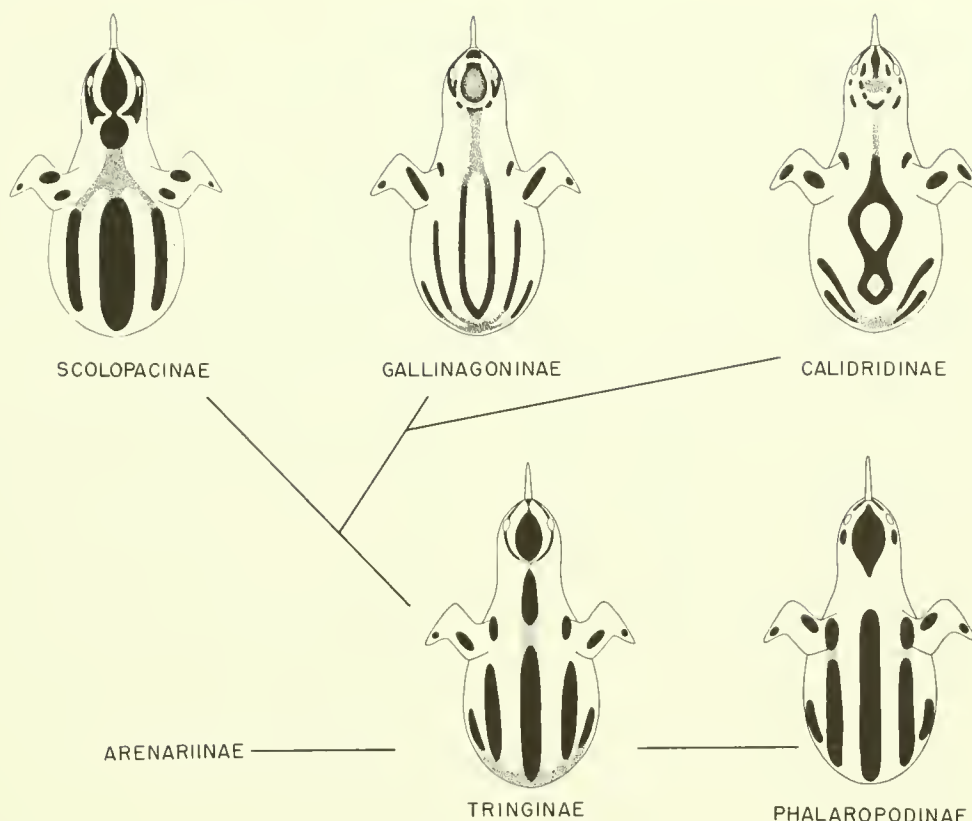


Fig. 30. Phenetic relationships of subfamilies in the Scolopacidae indicated by the patterns of the downy young.

Lowe's (1931b) placement of *Limnocryptes* and *Coenocorypha* with the snipe is supported by the chick plumages. Downy young of *Limnodromus* also resemble young snipe, which supports Lowe's contention that dowitchers are aberrant snipe. Some authors (e.g., Kozlova, 1962) have considered dowitchers most closely allied to the godwits (*Limosa*), but the only evidence for this is similarity in external morphology between adults of *Limnodromus semipalmatus* and *Limosa lapponica*. This is an outstanding example of convergence (Rand, 1950; see also Pitelka, 1948; Sutton, 1949). The color, pattern, and feather structure of young godwits are entirely unlike those of dowitchers and cannot be transformed easily into those of dowitchers. Further, the breeding behavior of *Limosa* (*limosa*: Lind, 1961; *haemastica*, pers. obs.) is unlike that of *Limnodromus* (*griseus*; pers. obs.), further negating close relationship of these genera.

CALIDRIDINAE

This group has been recognized as a distinct subfamily by most workers, although Verheyen (1958a) considered it a tribe of the Tringinae. Calidridine chicks are snipe-like in color and

feather structure and bear no similarity to tringine chicks. The easy transformation of a snipe pattern to a calidridine pattern — by fusing the paired lines at midback — is further evidence for close relationship.

As noted, two slightly different types of calidridine downy plumages can be recognized, but these seem to be of no taxonomic value. Certainly any grouping that separates *bairdii* from *fuscicollis*, *maritima* from *ptiloenemis*, and *subruficollis* from *pugnax* must be suspect. I infer that selection on chicks in the first group has been toward crypsis; these species tend to nest in wet marshes, where the chicks are usually hidden by the vegetation. The more strongly marked and contrasting plumages of chicks in the second group reflect secondary selection for disruptive coloration. These species tend to nest in drier, more open habitats, where the chicks may be more conspicuous. Other lines of evidence will be needed to sort out relationships in this subfamily.

PHALAROPODINAE

Peters (1934) and others (e.g., Larson, 1957) have considered the phalaropes allies of the recurvirost-

rids, but there is no evidence for that assumption. Skull characters (Lowe, 1931b: 758) and chick patterns both indicate that phalaropes are tringine derivatives. I place this group as a subfamily of the Scolopacidae.

Relationships within the Scolopacidae are diagrammed in Figure 30.

The arrangement of phalarope species accepted by the A.O.U. (1957) has been criticized by Bull (1964: 222), whose arrangement (*fulicarius*, *lobatus*, *tricolor*) is a decided improvement. Yet, if the trend in phalarope evolution can be assumed to be from a tringine-like ancestor toward more aquatic forms, as seems likely, the reverse order is preferable. Of the three species, *tricolor* is morphologically and behaviorally most similar to the tringine sandpipers, whereas *lobatus* and *fulicarius* are more specialized for an aquatic existence. Because *fulicarius* is the most highly marine of the species, it seems to be most different from the tringine stock and, therefore, should be placed last in the sequence.

Interfamilial Relationships

Sandpipers have always been considered most closely allied to plovers, and many workers (e.g., Hartert, 1912-1921) have placed these groups (and others) into a single family. According to Lowe (1931b: 733), this merging has been based largely on external similarities. I infer that the previously assumed "intermediacy" of *Arenaria* and *Aphriza* must also have been important. Yet, Lowe (1931b: 733-738) listed anatomical characters indicating a "more deep-seated" distinction between the Scolopacidae and Charadriidae, and this view is supported by the chick plumages. In spite of their diversity, there are no patterns in the Scolopacidae that resemble those of the Charadriidae and, furthermore, simple transformations of pattern do not seem probable. It would be far simpler to derive a *Tringa*-like pattern from the striped pattern of the Jacanoidea.

The relationships of the Scolopacidae should be

re-examined. Even if sandpipers are most closely allied to plovers, their divergence dates from at least the Oligocene (see below), and the radiation in each line has been extensive. Those who would lump these families should, on the basis of consistency, also place the Burhinidae, Haematopodidae, Ibidorhynchidae, Recurvirostridae, and Glareolidae as subfamilies in an expanded family Charadriidae (*cf.* Mayr and Amadon, 1951; Yudin, 1965). I fail to see any advantage in such extreme lumping. I retain the Scolopacidae as a distinct family.

THINOCORIDAE, CHIONIDIDAE

Relationships of the Thinocoridae cannot be inferred from the plumages of their chicks. Young of *Attagus* are very plover-like, and the color and pattern of *A. malouinus* is much like that of *Charadrius falklandicus*; however, a very young chick of *falklandicus*, is not available and an adequate comparison cannot be made. Lowe (1931b: 728) described seed-snipe chicks as calidridine-like, but the resemblance is found only in *Thinocorus* and results from similarities in feather structure discussed above.

Downy Sheathbills are unlike other wader chicks, although they bear a vague similarity to plover (or gull) chicks. Lowe (1916b, 1931b: 763) suggested that this family formed a "connecting bridge between the Skuas and the Limicolae proper," and grouped it with the Dromadidae and Glareolidae in his suborder Laro-Limicolae. Most other workers place the Chionididae next to the Thinocoridae, and Yudin (1965) combined both families into a single superfamily. The downy young neither support nor contradict this merging, but anatomical, morphological, and behavioral characters, as well as inferences from geographic distribution (Yudin, 1965), provide some support for Yudin's interpretation. I follow him in recognizing but a single superfamily, Chionidoidea, for both families.

PHYLOGENY

The fossil record of the Charadrii is poor, several families being entirely unrepresented to date (Brodkorb, 1967). Further, the correct taxonomic allocation of some of the earliest remains is highly questionable. Yet, in spite of these difficulties, the limited data, taken in conjunction with the relationships suggested in the preceding discussion, can be used to attempt a preliminary, though *highly speculative* reconstruction of shorebird phylogeny (Fig. 31).

By the late Cretaceous at least two groups of shorebirds were already in existence. One of these, the Cimlopterygidae (four species, two genera; Brodkorb, 1963) shows similarities to the recurvirostrids and presumably was directly ancestral to the Eocene forms *Coltonia* and *Presbyornis* (now placed in a subfamily, Presbyornithinae, of the Recurvirostridae; Brodkorb, 1967). The other group, the Palaeotringinae (five species, one genus; Brodkorb, 1967) has been placed in the Scolopacidae (Wetmore, 1956; Brodkorb, 1967), but its allocation seems far less certain. Shufeldt (1915) suggested that two species of *Palaeotringa*, *littoralis* and *vagans*, may have been larvae; a third, *vetus*, may have been a "Woodcock (or Snipe?) . . . but it just as likely to have been a very large Plover, or a Godwit, or some other limicoline form, though certainly no species of *Tringa* like our existing sandpipers" (p. 24). Shufeldt further suggested that two Middle Eocene species, *gracilis* and *bellus*, assigned by Marsh (1872: 258) to the catch-all genus *Aletornis* (included by Wetmore, 1956, in the Gruidae) were limicoline. Of *bellus*, Shufeldt writes (1915: 29) "there is not enough of the specimen, however, to make even an approximate guess as to what kind of a small limicoline bird it may have belonged to in life. It is just as likely to have been a small Plover, or a Snipe of a similar size, and so on." Of *gracilis*, he comments (p. 30) "so imperfect is this fragment, however, and so little is there of it that it is quite impossible to state with certainty that it belonged to a *Philohela*, either a living or an extinct species; it is quite possible for it to have belonged to some kind of a *Snipe* of a like size." Brodkorb (1967), without stated reason, included these species in *Palaeotringa*. There appears to be no reason to consider *Palaeotringa* as mono-

phyletic, and all that I can infer about the Palaeotringinae (*sensu* Brodkorb, 1967) is that it includes all the early charadriiform-like birds that show no close resemblance to the Cimlopterygidae. A modern, critical review of this group is needed.

Rapid radiation seems to have characterized the Cimlopterygidae-Recurvirostridae line. By the Oligocene both subfamilies of the Charadriidae had been derived and, at least, by the Miocene the Haematopodidae and Burhinidae had appeared. The similar chick color patterns in the Haematopodidae, Burhinidae, and Recurvirostridae, therefore, presumably originated more than 25 million years ago (potassium-argon dating of Miocene deposits by Everenden et al., 1964). Whether *Ibidorhyncha* represents an early offshoot from this line or rapid recent divergence is unknown. The Thimocoridae and Chionididae, which may be ancient, presumably diverged from this line. The separation of the Glareolidae from the Charadriidae may have been relatively recent, judging by the morphological similarities between the families.

The radiation of the Scolopacidae began in the late Eocene; at this time tringine sandpipers and possibly godwits were present, although the earliest unquestioned record for *Limosa* is Miocene. I suspect that the Scolopacinae and Gallinagininae stem from an early radiation in temperate and tropical areas, whereas the Calidridinae, Phalaropodinae, Arenariinae probably radiated in arctic and subarctic regions, perhaps no earlier than the late Miocene (*cf.* Larson, 1957).

The ancestry of the Scolopacidae is not clear. Wetmore (1956) and Brodkorb (1967) consider the Palaeotringinae ancestral to modern scolopacids. If they are correct close relationship to plovers is precluded, and it would be desirable to recognize a new superfamily, Scolopacoidea, for this line. Until such a relationship is definitely established, it would seem preferable to retain the Scolopacidae in the Charadrioidea and to recognize the Palaeotringinae as a distinct, though artificial, family.

The Jacanoidea originated with the Rostratulidae in the Eocene and gave rise to the Jacanidae (includes Rhegminornithidae of Wetmore, 1934; see Brodkorb, 1967) by the Miocene.

Chick patterns do not clarify the interrelation-

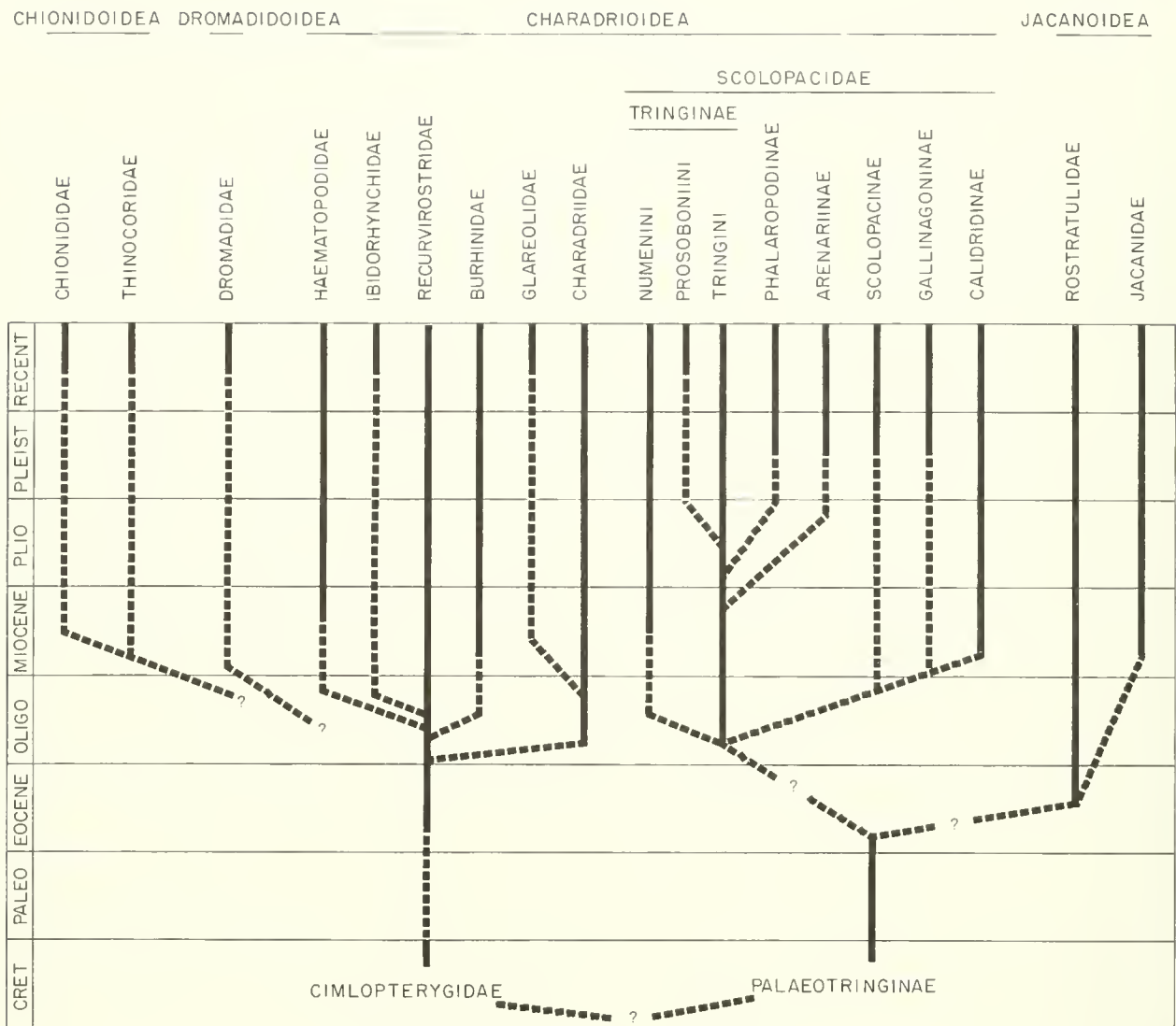


Fig. 31. A tentative phylogeny of the Charadrii.

ships of the four superfamilies here recognized. Chicks of the Dromadoidea are unpatterned. The Charadrioidae, as noted, may be polyphyletic: patterns in the Cimlopterygidae-Recurvirostridae line are unlike those of other waders, except that plover chicks somewhat resemble those of the Thinocoidea; patterns in the line leading to the Scolopa-

cidae could have been derived from those of the Jacanoidea (or vice-versa).

Although it is impossible to reconstruct a primitive chick color pattern for the Charadrii, it would seem almost certain that young of the ancestral wader bore a striped dorsal pattern.

CLASSIFICATION

Although the aim of this study has not been to revise shorebird classification but to clarify relationships among the higher taxa, the reinterpretations indicated by chick plumages that are supported by additional evidence have been incorporated into the classification proposed in Table 2.

In a linear classification, "primitive" forms (i.e., forms bearing the greatest number of primitive characters) are in theory listed first in each taxon. Since there are rarely adequate bases for determining primitiveness — certainly it cannot be inferred from an incomplete fossil record — the arrangement of taxa is usually no more than convention. Furthermore, while a linear classification can be used to indicate relationships in the simplest groups, in groups like the Charadrii, in which there

has been extensive radiation, it is inadequate. Even were the phylogeny of the Charadrii known, it would be impossible to linearly arrange shorebird taxa in a fully consistent and meaningful manner. What is critical, however, is not classification, which is subject to constant revision, but relationships, which are unchanging. With an understanding of relationships a stable, though partly arbitrary, classification can be established. In the interests of eventual stability, the classification used here adheres to Peters' (1934) arrangement as closely as possible, both in order, ranking, and arrangement of taxa. Inferences regarding relationship or phylogeny must not be drawn from this classification, but from the text, where the evidence is discussed.

TABLE 2
A CLASSIFICATION OF RECENT CHARADRII

Suborder **CHARADRII**Superfamily **JACANOIDEA**Family **JACANIDAE**

Genus: *Microparra*, *Actophilornis*, *Irediparra*, *Hydrophasianus*, *Metopidius*, *Jacana*

Family **ROSTRATULIDAE**

Genus: *Rostratula*, *Nycticryphes*

Superfamily **DROMADOIDEA**Family **DROMADIDAE**

Genus: *Dromas*

Superfamily **CHARADRIOIDEA**Family **HAEMATOPODIDAE**

Genus: *Haematopus*

Family **IBIDORHYNCHIDAE**

Genus: *Ibidorhyncha*

Family **RECURVIROSTRIDAE**

Genus: *Himantopus*, *Cladorhynchus*, *Recurvirostra*

Family **BURHINIDAE**

Genus: *Burhinus*, *Esacus*

Family **GLAREOLIDAE**Subfamily **CURSORIINAE**

Genus: *Pluvianus*, *Rhinoptilus*, *Peltohyas*, *Cursorius*

Subfamily **GLAREOLINAE**

Genus: *Stiltia*, *Glareola*

Family **CHARADRIIDAE**Subfamily **VANELLINAE**

Genus: *Vanellus*

Subfamily **CHARADRIINAE**

Genus: *Charadrius*, *Anarhynchus*, *Phegornis*, *Pluvialis*, *Eudromias*, *Oreopholus*, *Pluvianellus*

Family **SCOLOPACIDAE**Subfamily **TRINGINAE**Tribe **NUMENINI**

Genus: *Limosa*, *Numenius*, *Bartramia*

Tribe **TRINGINI**

Genus: *Tringa*, *Catoptrophorus*, *Xenus*, *Actitis*, *Heteroscelus*

Tribe **PROSOBONINI**

Genus: *Prosobonia*

Subfamily **ARENARIINAE**

Genus: *Arenaria*

Subfamily **PHALAROPODINAE**

Genus: *Phalaropus*

Subfamily **SCOLOPACINAE**

Genus: *Scolopax*

Subfamily **GALLINAGONINAE**

Genus: *Coenocorypha*, *Gallinago*, *Lymnocyptes*, *Limnodromus*

Subfamily **CALIDRIDINAE**

Genus: *Aphriza*, *Calidris*, *Eurynorhynchus*, *Limicola*, *Micropalama*, *Tryngites*, *Philomachus*

Superfamily **CHIONIDOIDEA**Family **THINOCORIDAE**

Genus: *Attagus*, *Thinocorus*

Family **CHIONIDIDAE**

Genus: *Chionis*

SUMMARY

This study of relationships in the Suborder Charadrii is based primarily on a single character complex, the color patterns of the downy plumages of the chicks. These patterns function primarily, if not exclusively, to reduce the chicks' conspicuousness. Despite this role, the patterns are conservative; there is no evidence for convergence in pattern, except that convergence due to *pattern loss* occurs in association with nesting on uniformly colored substrates in several groups.

Color patterns of shorebird chicks are useful in showing relationships from the generic to the familial level; at the superfamilial level the patterns are too divergent, and at the specific level too similar to be of much taxonomic importance. In general, it may be stated that within any genus chick patterns are consistent and highly diagnostic, and that patterns are similar in closely related genera. Thus, the patterns may be used: 1) to place forms whose affinities are not known with certainty, 2) to suggest possible interrelationships of genera (and sometimes higher taxa), and 3) to indicate where presently accepted views of relationships need reinvestigation.

The following are the major relationships indicated by this study.

1. The Rostratulidae are most closely allied to the Jacanidae; these families are not closely allied to other shorebird families.

2. The Burhinidae are allied to the Haematopo-

dididae and Recurvirostridae.

3. There is no evidence to link *Ibidorhyncha* most closely to the Recurvirostridae.

4. The Glareolidae are closely allied to the Charadriidae. *Peltohyas* is a courser; *Rhinoptilus* may not be a natural taxon.

5. The Charadriidae are allied to the Recurvirostridae and Haematopodidae. *Phegornis* is a plover.

6. The Scolopacidae, which do not seem to be closely allied to the Charadriidae, comprise six subfamilies. The Arenariinae (*Arenaria* only) are considered tringine offshoots. *Aphriza* is a calidridine sandpiper. The Tringinae comprise three tribes: Numenini, Tringini, and Prosoboniini. The Phalaropodinae are derived from the Tringini, as are the Scolopacinae (*Scolopax* only). The Gallinagoninae (snipe and allies) are related to the Calidridinae; their affinities to the Scolopacinae seem distant. *Limnodromus* is a member of the Gallinagoninae and is not closely related to *Limosa*.

7. Chick patterns do not clarify the relationships of the Dromadidae, Thinocoridae, and Chionididae.

A revised classification of the Charadrii, to the genus level, is proposed in Table 2.

References to detailed descriptions of the downy plumages of individual species are given in the Appendix.

APPENDIX

REFERENCES TO DESCRIPTIONS AND ILLUSTRATIONS
OF DOWNY YOUNG SHOREBIRDS

I have listed here the location of descriptions, photographs, and other illustrations for the young of each species. Descriptions are given for those species examined that have not been described previously, or for which the published descriptions are inadequate. The term "Text Fig." refers to illustrations in the body of this paper. The following abbreviations are used: AMNH, American Museum of Natural History; BMNH, British Museum (Natural History); CNHM, Chicago Natural History Museum; ROM, Royal Ontario Museum; UMMZ, University of Michigan Museum of Zoology; USNM, United States National Museum.

This is not a complete listing of all descriptions of downy shorebirds. For the more commonly described forms I have included only those references that are generally available. Descriptions judged to be of special usefulness are indicated by an asterisk. Citations are given in abbreviated form and are not listed again in the bibliography unless they also appear in the preceding main text. Certain standard reference works (Bent, A.C., Life Histories of North American Shore Birds, Pt. 1, 1927; Pt. 2,

1929. Mackworth-Praed, C.W., and C.H.B. Grant, Birds of Eastern and Northern Africa, African Handbook of Birds, Series 1, Vol. 1, 1957; Birds of the Southern Third of Africa, African Handbook of Birds, Series 2, Vol. 1, 1962. Ridgway, R., Birds of North and Middle America, Pt. 8, 1919. Sharpe, R.B., Catalogue of Birds in the British Museum, Vol. 24, 1896. Witherby, H.F., F.C.R. Jourdain, N.F. Ticehurst, and B.W. Tucker, The Handbook of British Birds, Vol. 4, 1940) appearing often are given the briefest possible citation.

The arrangement followed for the major taxa within the Charadrii is that proposed in the main text. In most cases species' limits and the linear arrangement of species within genera follow Peters (1934); departures are explained in the text.

I have tried to provide references to the descriptions of the young of all species, but descriptions for some apparently do not exist and I have doubtless overlooked others. Readers knowing of omissions or of the location of specimens of apparently undescribed young are urged to inform me so that a complete list can be prepared.

Superfamily JACANOIDEA

Family JACANIDAE

Microparra capensis. Apparently undescribed; probably like *Actophilornis africana* (cf. Chapin, Bull. Amer. Mus. Nat. Hist. 75: 59, 1939).

Actophilornis africana. Description: Pitman, Bull. Brit. Ornith. Club 80: 104, 1960*; Mackworth-Praed and Grant, 1962: 279. Photograph: Text Fig. 3. Drawing: Pitman, *op. cit.*, p. 104.

Actophilornis albinucha. Description: AMNH no. 410615. Lac Kinkony, Madagascar. Forehead whitish; crown patch pale chestnut, bordered laterally and posteriorly by a black line from temporal canthus to occiput. Neck mainly whitish, but with thin black stripe along nape from occiput to upper back. Back deep chestnut; broad chestnut middorsal stripe bordered laterally by thin white, black stripes. Sides, top of thigh, wings, deep chestnut. Venter, sides of face, white. Photograph: Text Fig. 3.

(Note that young of this species differ considerably from those of *A. africana*.)

Irediparra gallinacea. Description: D'Ombra in Potter, Emu 33: 304-305, 1934. Photograph: Potter, *op. cit.*, p. 304; Hindwood, Emu 39: Pl. 37 (opp. p. 267), 1940; Text Fig. 26.

Hydrophasianus chirurgus. Description: Hoffman, Zool. Jahrb. (Syst.) 78: 393, 1949. Photograph: Hoffman, *op. cit.*, p. 393.

Metopidius indicus. Description: Sharpe, 1896: 74.

Jacana spinosa. Description: Sharpe, 1896: 87*; Sharpe in Ridgway, 1919: 9*.

Family ROSTRATULIDAE

Rostratula benghalensis. Description: Hindwood, Austr. Bird Watcher 1: 68-69, 1960*; Elgood and Donald, Ibis 104: 255, 1962. Photograph: Hindwood, *op. cit.*, p. 67; Text Fig. 26. Color Plate: Blyth in Jardine, Contr. to Ornith., 1852: Pl. 89, p. 53.

Nycticryphes semicollaris. Apparently undescribed. Drawing: Pereyra, "Neustras Aves." p. 180, 1943.

Superfamily DROMADOIDEA

Family DROMADIDAE

Dromas ardeola. Description: Sharpe, 1896: 29*; Lowe, Ibis 1916: 320-321*; Mackworth-Praed and Grant, 1962: 341.

Superfamily CHARADRIOIDEA

Family HAEMATOPODIDAE

Haematopus ostralegus. Description: Witherby *et al.*, 1940: 419*. Color Plate: Witherby *et al.*, 1940: Pl. 124 (opp. p. 414).

Haematopus palliatus. Description: Ridgway, 1919: 33*; Webster, Wilson Bull. 55: 41-42, 1943. Photograph: Text Fig. 4.

Haematopus bachmani. Description: Webster, Wilson Bull. 55: 42, 1943. Photograph: Webster, Condor 44: 205-206, 1942; Text Fig. 4.

Haematopus leucopodus. Description: Webster, Wilson Bull. 55: 42-43, 1943.

Haematopus fuliginosus. Description: Webster, Wilson Bull. 55: 44, 1943. Photograph: Mellor and White, Emu 12: Pl. 26 (opp. p. 160), 1913.

Haematopus ater. Description: Webster, Wilson Bull. 55: 42, 1943.

Family **IBIDORHYNCHIDAE**

Ibidorhyncha struthersii. Description: Johansen, Ornith. Monats. 15: 99-100, 1907; Ludlow, Ibis 1928: 222*; Baker, J. Bombay Nat. Hist. Soc. 35: 481, 1932*. Photograph: Ludlow and Kinnear, Ibis 1934: Pl. 3 (opp. p. 114).

Family **RECURVIROSTRIDAE**

Himantopus himantopus subsp. Description: Baker, J. Bombay Nat. Hist. Soc. 35: 476, 1932* (*himantopus*); Witherby *et al.*, 1940: 407* (*himantopus*); Oliver, "New Zealand Birds," pp. 301, 304, 1955 (*leucocephalus, novaezelandiae*); Ridgway, 1919: 442-443 (*mexicanus*); Housse, "Las Aves de Chile," p. 131, 1945 (*melanurus*). Photograph: Hindwood, Emu 39: Pl. 25 (opp. p. 225), 1940 (*leucocephalus*); Bent, 1927: Pl. 12 (*mexicanus*); Text Fig. 20 (*mexicanus*).

Cladorhynchus leucocephalus. Description: Glauert and Jenkins, J. Roy. Soc. Austr. 17: 3, 1931; Serventy and Whittell, "Handbook of Birds of Western Australia," 3 ed., p. 205, 1962.

Recurvirostra avosetta. Description: Baker, J. Bombay Nat. Hist. Soc. 35: 479, 1932*; Witherby *et al.*, 1940: 412-413*. Color Plate: Witherby *et al.*, 1940: Pl. 120 (opp. p. 348).

Recurvirostra americana. Description: Bent, 1927: 40*. Photograph: Bent, 1927: Pl. 8; Text Fig. 20. Color Plate: Brooks in Allen, Natl. Geog. Mag. 72: Pl. 12 (p. 214), 1937.

Recurvirostra novaehollandiae. Description: Chaffer, Emu 40: 127, 1940. Photograph: Chaffer, *op. cit.*, Pl. 30 (opp. p. 124).

Recurvirostra andina. Description: Sharpe, 1896: 24.

Family **BURHINIDAE**

Burhinus oedinenus. Description: Meinertzhagen, Ibis 1924: 335-336; Witherby *et al.*, 1940: 435*. Photograph: Bird, Brit. Birds 27: 114, 1933. Wadewitz, Beitr. z. Vogelk. 4: 97-101, 1955; Text Fig. 22. Color Plate: Witherby *et al.*, *op. cit.*, Pl. 123 (opp. p. 396).

Burhinus senegalensis. Description: Meinertzhagen, Ibis 1924: 341.

Burhinus vermiculatus. Description: Meinertzhagen, Ibis 1924: 342; Mackworth-Praed and Grant, 1962: 277.

Burhinus capensis. Description: Mackworth-Praed and Grant, 1962: 276. Photograph: Carter, Afr. Wildlife 10: 68, 1956; Maclean, Ostrich, Supp. 6: 159, 1966.

Burhinus bistriatus. Description: Ridgway, 1919: 21*.

Burhinus superciliosus. Apparently undescribed.

Burhinus magnirostris. Description: Mathews and Iredale, "Manual Bds. Austr." Vol. 1, p. 116, 1921; Meinertzhagen, Ibis 1924: 350-351. Photograph: Burrell, Emu 8: 150, Pl. 14, 1909. Color Plate: Mathews and Iredale, *op. cit.*, Pl. 7 (opp. p. 180).

Esacus recurvirostris. Description: Ticehurst, Bull. Brit. Ornith. Club 43: 72, 1922; Deignan, U.S. Natl. Mus. Bull. 186: 130, 1945. Photograph: Text Fig. 22.

Esacus magnirostris. Apparently undescribed.

Family **GLAREOLIDAE**Subfamily **CUSORIINAE**

Pluvianus aegypticus. Description: Butler, Ibis 1931: 345*; Mackworth-Praed and Grant, 1962: 340. Photograph: Text Fig. 23.

Rhinoptilus africanus. Apparently undescribed. Photograph: Text Fig. 26.

Rhinoptilus cinctus. Apparently undescribed.

Rhinoptilus chalcopterus. Apparently undescribed. Photograph: Steyn, Afr. Wildlife 20: 242, 1966.

Rhinoptilus bitorquatus. Apparently undescribed.

Peltahyas australis. Description: North, "Nests and eggs of Australian Birds," Vol. 4, p. 289, 1913; Serventy and Whittell, "Handbook of Birds of Western Australia," 2 ed., p.

157, 1951. Photograph: Text Fig. 24.

Cursorius cursor. Description: Meinertzhagen, Ibis 1927: 474; Witherby *et al.*, 1940: 424*.

Cursorius coromandelicus. Description: Ticehurst, J. Bombay Nat. Hist. Soc. 31: 376, 1926. Photograph: Phillips, J. Bombay Nat. Hist. Soc. 43: Pl. 2 (opp. p. 202), 1942.

Cursorius temminckii. Description: Steyn, Afr. Wildlife 19: 32, 1965. Photograph: Steyn, *op. cit.*, p. 32; Text Fig. 23.

Subfamily **GLAREOLINAE**

Stiltia isabella. Description: MacGillivray, Emu 24: 84, 1924; Bailey, Emu 35: 5, 1935; Chaffer, Emu 49: 2, 1949. Photograph: Chaffer, *op. cit.*, Pl. 2 (opp. p. 2).

Glareola pratincola. Description: Ticehurst, J. Bombay Nat. Hist. Soc. 31: 377, 1926. Muller, Ornith. Beob. 45: 116, 1948; Witherby *et al.*, 1940: 427*. Photograph: Muller, *op. cit.*, p. 118.

Glareola maldivarum. Description: Baker, J. Bombay Nat. Hist. Soc. 34: 8, 1930.

Glareola nordmanni. Apparently undescribed.

Glareola ocularis. Apparently undescribed.

Glareola nuchalis. Description: Chapin, Bull. Amer. Mus. Nat. Hist. 75: 119, 1939*; Mackworth-Praed and Grant, 1962: 338. Photograph: Text Fig. 23.

Glareola lactea. Description: Ticehurst, J. Bombay Nat. Hist. Soc. 31: 377, 1926.

Glareola cinerea. Description: Chapin, Bull. Amer. Mus. Nat. Hist. 75: 120-121, 1939.

Family **CHARADRIIDAE**Subfamily **VANELLINAE**

Vanellus vanellus. Description: Witherby *et al.*, 1940: 402. Color Plate: Witherby *et al.*, *op. cit.*, Pl. 123 (opp. p. 396).

Vanellus crassirostris. Apparently undescribed.

Vanellus armatus. Description: Mackworth-Praed and Grant, 1962: 297.

Vanellus spinosus. Description: Mackworth-Praed and Grant, 1962: 296.

Vanellus duvaucelii. Description: USNM no. 336804. Ban Pa Lu'at, Siam. Dorsal surface of head sand-colored; forehead unmarked, rest irregularly mottled with black. Small black dot on lores; broad black band from posterior corner of eye encircling occiput. Nape, venter, distal end of wing, white. Back, proximal part of wing, sand-colored, lightly dotted with black. Narrow, interrupted, black V-shaped figure on back, with apex at rump; black band from hip to tail borders sandy area postero-laterally. Photograph: Text Fig. 5.

Vanellus tectus. Description: Mackworth-Praed and Grant, 1957: 363-364. Photograph: Text Fig. 5.

Vanellus malabaricus. Apparently undescribed.

Vanellus albiceps. Apparently undescribed.

Vanellus lugubris. Description: Mackworth-Praed and Grant, 1962: 294-295.

Vanellus melanopterus. Description: Mackworth-Praed and Grant, 1962: 295.

Vanellus coronatus. Description: Symmes, Ostrich 23: 87, 1952; Mackworth-Praed and Grant, 1962: 293; van Someren, Fieldiana: Zoology, 38: 123.

Vanellus senegallus. Description: Mackworth-Praed and Grant, 1962: 299.

Vanellus melanoccephalus. Apparently undescribed.

Vanellus superciliosus. Apparently undescribed.

Vanellus gregarius. Description: Witherby *et al.*, 1940: 395*.

Vanellus leucurus. Apparently undescribed.

Vanellus cayanus. Apparently undescribed.

Vanellus chilensis. Description: UMMZ no. 75328, Horqueta, Paraguay; UMMZ no. 157267, Buenos Aires Prov., Argentina. Dorsal surface of head, sides of face including malar

region, lower part of nape, proximal portion of wings, and back grayish brown, mottled with black in no apparent pattern. Wing tips, throat, belly, and narrow band crossing upper part of nape white; chest crossed by large, black band. Head mottling sharply demarcated posteriorly by black band from auriculars to occiput. In one specimen, thin black lines in shoulder region form an indistinct V, with its apex at midback (this region not visible in other specimen). Interrupted black lines lead from hip to tail; black stripe along lateral surface of thigh. Photograph: Text Fig. 5.

Vanellus resplendens. Apparently undescribed.

Vanellus cinereus. Apparently undescribed. Photograph: Fushihara, *Tori* 15: 163, 1959.

Vanellus indicus. Description: Baker, *J. Bombay Nat. Hist. Soc.* 31: 377, 1926*.

Vanellus macropterus. Apparently undescribed.

Vanellus tricolor. Description: Lord, *Emu* 51: 79, 1951; Gerrits, *Avicult. Mag.* 62: 222, 1956*. Photograph: Gerrits, *op. cit.*, Pl. 2 (opp. p. 223). Color Plate: Mathews and Iredale, "Manual Bds. Australia," Vol. 1, Pl. 6, 1921.

Vanellus miles. Description: Oliver, "New Zealand Birds," p. 271, 1955. Photograph: Oliver, *op. cit.*, p. 271; Sansom, *Notornis* 5: Pl. 38 (opp. p. 207), 1954. Color Plate: Mathews and Iredale, "Manual Bds. Australia," Vol. 1, Pl. 6, 1921.

Subfamily CHARADRIINAE

Charadrius hiaticula. Description: Witherby *et al.*, 1940: 352*; Ridgway, 1919: 120*. Color Plate: Witherby *et al.*, 1940: Pl. 120 (opp. p. 348).

Charadrius semipalmatus. Description: Ridgway, 1919: 116*. Photograph: Bent, 1929, Pl. 38; Text Fig. 7.

Charadrius placidus. Apparently undescribed.

Charadrius dubius. Description: Witherby *et al.*, 1940: 358*. Color Plate: Witherby *et al.*, 1940: Pl. 120 (opp. p. 348).

Charadrius wilsonia. Description: Ridgway, 1919: 109*. Photograph: Bent, 1929, Pl. 48; Text Fig. 7.

Charadrius vociferus. Description: Ridgway, 1919: 99-100*. Photograph: Bent, 1929, Pl. 34; Text Fig. 7.

Charadrius melodus. Description: Ridgway, 1919: 129*. Photograph: Bent, 1929, Pl. 42.

Charadrius thoracicus. Apparently undescribed.

Charadrius pecuarius. Description: Mackworth-Praed and Grant, 1957: 344. Photograph: Text Fig. 6.

Charadrius sanctaehelenae. Apparently undescribed.

Charadrius tricoloris. Description: Mackworth-Praed and Grant, 1962: 288.

Charadrius alexandrinus. Description: Ridgway, 1919: 137*. Photograph: Bent, 1929, Pl. 45; Text Fig. 6. Color Plate: Witherby *et al.*, 1940: Pl. 120 (opp. p. 348).

Charadrius marginatus. Apparently undescribed.

Charadrius peronii. Description: AMNH no. 346566. Melolo, Sumba Is. (Indonesia). Forehead, sides of face, nape, wing tips, and entire venter white. Crown pale sandy buff, with black flecks forming thin midcrown stripe and narrow posterior border to crown patch. Back sand-colored with light black flecking; rump bordered by thin black stripe from hip to tail. Wings sandy to wrist; broad black band paralleling ulna, narrow band paralleling radius. Photograph: Text Fig. 6.

Charadrius venustus. Description: Mackworth-Praed and Grant, 1957: 343*.

Charadrius collaris. Apparently undescribed.

Charadrius bicinctus. Description: Oliver, "New Zealand Birds," p. 259-260, 1955. Photograph: Oliver, *op. cit.*, p. 261; Soper, *Notornis* 9: 126, 1961.

Charadrius falklandicus. Description: Cawkell and Hamilton, *Ibis* 103a: 18, 1961; Brooks, *Bull. Mus. Comp. Zool.* 61: 151,

1917. AMNH no. 443950. Stanley, Falkland Islands. One well-grown chick. Head and back buffy white, uniformly mottled with heavy black markings; no pattern detectable, except for short transverse band at the tail. Forehead buffy, unmarked. Nape pale rufous. Sides of face buffy; thin black line from base of upper mandible to anterior corner of eye, then passing dorsally onto crown; interrupted malar stripe from base of lower mandible to auriculars. Underparts dirty white, perhaps slightly buffier on chest. Photograph: Text Fig. 7.

Charadrius mongolus. Description: Baker, *J. Bombay Nat. Hist. Soc.* 4: 874, 1930*; Ridgway, 1919: 133*.

Charadrius leschenaultii. Description: Mathews, *Emu* 33: 17, 1933*.

Charadrius asiaticus. Description: Ingram *in* Witherby *et al.*, 1940: 383.

Charadrius veredus. Apparently undescribed.

Charadrius modestus. Description: Brooks, *Bull. Mus. Comp. Zool.* 61: 151, 1917. Photograph: Text Fig. 26.

Charadrius montanus. Description: Ridgway, 1919: 106*. Photograph: Bent, 1929, Pl. 56; Text Fig. 6.

Charadrius melanops. Description: Mathews and Iredale, "Manual Bds. Austr.," Vol. 1, p. 174, 1921. Photograph: Littlejohns, *Emu* 31: Pl. 5 (opp. p. 16), 1931; MacKenzie, *Notornis* 9: 281, 1962*. Color Plate: Mathews and Iredale, *op. cit.*, Pl. 6.

Charadrius cinctus. Apparently undescribed.

Charadrius rubricollis. Apparently undescribed.

Charadrius novaseelandiae. Description: Sharpe, 1896: 305; Fleming, *Emu* 39: 9, 1939. Photograph: Fleming, *op. cit.*, Pl. 6 (opp. p. 9). Color Plate: Fleming, *op. cit.*, Pl. 1 (opp. p. 1); Forbes, *Ibis* 1893: Pl. 15 (opp. p. 529). The chick in Forbes' plate is unfortunately depicted with a well-developed hind toe; the species has only three toes.

Anarhynchus frontalis. Description: Oliver, "New Zealand Birds," p. 268, 1955.

Phegornis mitchellii. Description: Johnson, "Birds of Chile and adjacent regions of Argentina," p. 331, 1965; Johnson, *Ibis* 106: 250, 1964.

Pluvialis apricaria. Description: Ridgway, 1919: 81*; Witherby *et al.*, 1940: 368*. Color Plate: Witherby *et al.*, 1940: Pl. 121 (opp. p. 364).

Pluvialis dominica. Description: Ridgway, 1919: 84*; Bent, 1929: 180-181. Photograph: Text Fig. 8.

Pluvialis squatarola. Description: Ridgway, 1919: 73; Bent, 1929: 160*; Witherby *et al.*, 1940: 380. Photograph: Text Fig. 8.

Pluvialis obscura. Description: Oliver, "New Zealand Birds," p. 257, 1955.

Eudromia morinellus. Description: Witherby *et al.*, 1940: 388. Photograph: Text Fig. 8. Color Plate: Witherby *et al.*, 1940: Pl. 115 (opp. p. 290).

Oreopholus ruficollis. Description: Chubb, *Ibis* 1919: 261. Photograph: Text Fig. 8.

Pluvianellus socialis. Apparently unknown.

Family SCOLOPACIDAE

Subfamily TRINGINAE

Tribe NUMENINI

Limosa limosa. Description: Sharpe, 1896: 385; Witherby *et al.*, 1940: 165. Photograph: Haverschmidt, "The Black-tailed Godwit," 1963: Pl. 15 (opp. p. 69).

Limosa haemastica. Description: Hagar, *Living Bird* 5: 32, 1966. Photograph: Ellis, *Audubon Mag.* 50: 159, 1948; Congdon and Congdon, *Canad. Field-Nat.* 66: 143, 1952; Congdon, *Condor*, 54: 291, 1952; Text Fig. 9. Color Plate: Sutton *in* Hagar, *op. cit.*; Frontis.

Limosa lapponica. Description: Bent, 1927: 291-292*; Witherby *et al.*, 1940: 195*. Photograph: Bent, *op. cit.*, Pl. 50. Color Plate: Vorobiev, "Ptitsy Yakutii," Acad. Sci. U.S.S.R. (Moscow), Pl. 42, 1963.

Limosa fedoa. Description: Bent, 1927: 282.

Numenius minutus. Description: Oliver, "New Zealand Birds," p. 298, 1955. Color Plate: Turgarinov, J. f. Ornith. 77 (II. Festschrift E. Hartert): Pl. 1 (opp. p. 142), 1929.

Numenius borealis. Downy young unknown.

Numenius phaeopus. Description: Ridgway, 1919: 399; Taverner and Sutton, Ann. Carnegie Mus. 23: 36-37, 1934. Photograph: Bent, 1929: Pl. 21; Text Fig. 9. Color Plate: Taverner and Sutton, *op. cit.*, Frontis; Witherby *et al.*, 1940: Pl. 105 (opp. p. 172).

Numenius tahitiensis. Description: Allen and Kyllingstad, Auk 66: 346-349, 1949. Photograph: Allen, Natl. Geog. Mag. 94: 762, 763, 1948 (color); Allen and Kyllingstad, *op. cit.*, Pl. 2 (opp. p. 344).

Numenius tenuirostris. Apparently undescribed.

Numenius orquata. Description: Witherby *et al.*, 1940: 171*. Color Plate: Witherby *et al.*, *op. cit.*, Pl. 105 (opp. p. 172).

Numenius madagascariensis. Apparently undescribed.

Numenius americanus. Description: Ridgway, 1919: 39; Bent, 1929: 102. Photograph: Bent, *op. cit.*, Pl. 20.

Bartramia longicauda. Description: Ridgway, 1919: 380; Witherby *et al.*, 1940: 183. Photograph: Bent, 1927: Pl. 15; Text Fig. 9.

Tribe TRINGINI

Tringa erythropus. Description: Baker, J. Bombay Nat. Hist. Soc. 36: 298-299, 1932*; Witherby *et al.*, 1940: 335. Photograph: Text Fig. 10.

Tringa totanus. Description: Ridgway, 1919: 344; Baker, J. Bombay Nat. Hist. Soc. 36: 294, 1932*; Witherby *et al.*, 1940: 328. Color Plate: Witherby *et al.*, 1940: Pls. 115, 118 (opp. pp. 290, 318).

Tringa stagnatalis. Description: Gavrilenko, Bull. Soc. Nat. Moscow 60: 99, 1955 (not seen; reference from Zool. Record 1955: 23). ROM no. 38306, Pusztá Tzunyog, Hungary. Ground color of dorsal down buffy brown; sides of head, venter, whitish buff. Dorsum patterned with dark brown as in other tringine sandpipers except midback stripe does not extend to rump, and line from hip to rump more prominent than in other tringines.

Tringa nebularia. Description: Ridgway, 1919: 324; Witherby *et al.*, 1940: 340. Photograph: Nethersole-Thompson, "The Greenshank," 1951: Pls. 15, 21 (opp. pp. 132, 180). Color Plate: Witherby *et al.*, 1940: Pl. 119 (opp. p. 334).

Tringa guttifer. Description: Kuroda, Tori 9: 238, 1936. Photograph: Kuroda, *op. cit.*, p. 234. Color Plate: Kuroda, *op. cit.*, Pl. 4 (opp. p. 207).

Tringa melanoleuca. Description: Ridgway, 1919: 332; Bent, 1927: 325*. Photograph: Text Fig. 10. Drawing: Rowan, Brit. Birds 23: Pl. 4 (opp. p. 16), 1929.

Tringa flavipes. Description: Bent, 1927: 339; Rowan, Brit. Birds 23: 12-13, 1929. Photograph: Bent, *op. cit.*, Pl. 55; Text Figs. 10, 26. Drawing: Rowan, *op. cit.*, Pl. 3 (opp. p. 12).

Tringa solitaria. Description: Ridgway, 1919: 363*; Sutton in Bannerman, "Birds of the British Isles," 10: 84, 1961. (Sutton has correctly pointed out that the description in Bent, 1929: 4, actually refers to *Actitis macularia*.) Photograph: Text Fig. 10.

Tringa ocropus. Description: Baker, J. Bombay Nat. Hist. Soc. 36: 3, 1932; Witherby *et al.*, 1940: 314*. Photograph: Hasse and Wobus, Beitr. z. Vogelk. 9: 427, 1964. Color Plate: Witherby *et al.*, *op. cit.*, Pl. 117 (opp. p. 302).

Tringa glareola. Description: Ridgway, 1919: 348*; Baker, J.

Bombay Nat. Hist. Soc. 36: 10-11, 1932*; Witherby *et al.*, 1940: 309. Photograph: Kirchner, J. f. Ornith. 101: 342, 343, 1960; Barth, Brit. Birds 54: Pls. 22, 24, 25, 1961. Color Plate: Witherby *et al.*, *op. cit.*, Pl. 117 (opp. p. 302).

Catoptrophorus semipalmatus. Description: Ridgway, 1919: 316; Bent, 1929: 31*. Photograph: Tompkins, Wilson Bull. 77: 163, 1965.

Xenus cinereus. Description: Witherby *et al.*, 1940: 296*; Oliver, "New Zealand Birds," p. 291, 1955. Photograph: Hosking, Brit. Birds 52: Pls. 18, 19 (opp. p. 45), 1959; Text Fig. 12.

Actitis hypoleucos. Description: Witherby *et al.*, 1940: 301*. Color Plate: Witherby *et al.*, *op. cit.*, Pls. 115, 117 (opp. pp. 290, 302).

Actitis macularia. Description: Ridgway, 1919: 373*. Photograph: Bent, 1929: Pl. 17; Mousley, Auk 54: Pl. 28 (opp. p. 457), 1937; Text Fig. 12.

Heteroscelus brevipes. Description: Witherby *et al.*, 1940: 345. Photograph: Neufeldt, Krechmar, and Ivanov, Brit. Birds 54: Pl. 6, 1961; Vorobiev, "Ptitsy Yakutii," Acad. Sci. U.S.S.R. (Moscow), Pl. 50, 1963.

Heteroscelus incanus. Description: Bent, 1929: 44*. Photograph: Bent, *op. cit.*, Pl. 12; Weeden, Condor 67: 88, 1965; Text Fig. 12. Color Plate: Shortt, Wilson Bull. 59: Frontis., 1947.

Tribe PROSOBONIINI

Prosobonia cancellatus. Apparently undescribed.

Prosobonia leucoptera. Extinct. Downy young unknown.

Subfamily ARENARIINAE

Arenaria interpres. Description: Witherby *et al.*, 1940: 226*; Ridgway, 1919: 51; Parmelee and MacDonald, Nat. Mus. Canada Bull. 169, p. 42, 1960. Photograph: Bent, 1929: Pl. 56; Text Fig. 13.

Arenaria melanocephala. Description: Bent, 1929: 301*. Photograph: Text Fig. 13.

Subfamily PHALAROPODINAE

Phalaropus tricolor. Description: Ridgway, 1919: 431*. Photograph: Text Fig. 21.

Phalaropus lobatus. Description: Ridgway, 1919: 424; Bent, 1927: 21*. Photograph: Text Fig. 21. Color Plate: Witherby *et al.*, 1940: Pl. 107 (opp. p. 212).

Phalaropus fulicarius. Description: Ridgway, 1919: 418-419*; Bent, 1927: 7*; Witherby *et al.*, 1940: 217*. Photograph: Text Fig. 21.

Subfamily SCOLOPACINAE

Scolopax rusticola. Description: Sharpe, 1896: 676; Ridgway, 1919: 150-151; Witherby *et al.*, 1940: 191-192. Photograph: Text Fig. 17. Color Plate: Witherby *et al.*, *op. cit.*, Pl. 115 (opp. p. 290).

Scolopax mira. Apparently undescribed. This form has been recognized as a distinct species by Vaurie ("Birds of the Palearctic Fauna. Non-Passeriformes," p. 429-430, 1965).

Scolopax saturata. Apparently undescribed.

Scolopax celebensis. Apparently undescribed.

Scolopax rochussenii. Apparently undescribed.

Scolopax minor. Description: Ridgway, 1919: 156; Pettingill, Mem. Bost. Soc. Nat. Hist. 9 (2): 192-193, 323-324, 1936. Photograph: Bent, 1927: Pl. 16; Pettingill, *op. cit.*, Pl. 19; Text Fig. 17. Color Plate: Sutton in Pettingill, *op. cit.*, Pl. 12 (Frontis).

Subfamily GALLINAGONINAE

Coenocorypha aucklandica subsp. Description: Meinertzhagen, Ibis 1926, p. 515 (*aucklandica*); p. 516 (*pusilla*); Oliver, "New Zealand Birds," p. 274 (*pusilla*), p. 276 (*heugeli*), p. 278 (*aucklandica*), 1955. Color Plate: Forbes, Ibis 1893: Pl. 15 (opp. p. 529).

- Gallinago solitaria*. Apparently undescribed.
- Gallinago hardwickii*. Description: Deignan in Wolfe, Emu 54: 203, 1954*. Photograph: Text Fig. 16.
- Gallinago nemoricola*. Apparently undescribed.
- Gallinago stenura*. Apparently undescribed.
- Gallinago megala*. Description: Naumov, Ornithologia 4: 165-166, 1962. Photograph: Naumov, *op. cit.*, p. 167.
- Gallinago nigripennis*. Description: Mackworth-Praed and Grant, 1962: 309.
- Gallinago macrodactyla*. Description: AMNH no. 410590. Ivo-hibe, Madagascar. A well-feathered chick, similar in pattern and dorsal coloration to chicks of *G. gallinago*, but paler brown on the venter.
- Gallinago media*. Description: Sharpe, 1896: 629-630*; Ridgway, 1919: 163*; Baker, Fauna Brit. India 6: 262, 1929; Witherby *et al.*, 1940: 196*.
- Gallinago gallinago* subsp. Description: Bent, 1927: 86-87* (*delicata*); Witherby *et al.*, 1940: 202* (*gallinago*). Photograph: Mousley, Auk 52: Pl. 22 (opp. p. 410), 1935; Text Fig. 15. Color Plate: Witherby *et al.*, *op. cit.*, Pls. 106, 115 (opp. pp. 194, 290).
- Gallinago paraguaiae* subsp. Description: Meinertzhagen, Ibis 1926: 509 (*brasiliensis*). According to Meinertzhagen, the chick of *G. p. brasiliensis* is darker than that of *G. gallinago*. The chick of *G. p. andina* that I examined (CNHM no. 46836, Junin, Peru) is browner and lacks the extensive black markings of *gallinago*. The "bottle-brush" feathers are tipped with grayish buff, rather than white, and are inconspicuous. The dark throat markings are less extensive than in *gallinago*; the chin and belly are grayish buff, the chest pale cinnamon.
- Gallinago nobilis*. Description: Sharpe, 1896: 649; Meinertzhagen, Ibis 1926: 504. Photograph: Text Fig. 16.
- Gallinago undulata*. Apparently undescribed.
- Gallinago imperialis*. Downy young undescribed.
- Gallinago jamesoni*. Description: Meinertzhagen, Ibis 1926: 513.
- Gallinago stricklandii*. Description: AMNH no. 444209, Caroline Island, Chile. A well-feathered chick, 8-10 days old, similar to *Gallinago gallinago* in pattern, paler in color. Upper parts pinkish cinnamon with dark brown markings; "bottle-brush" feathers tipped with buff or grayish-white. Neck and chest pinkish cinnamon, belly paler; tiny dark spot on throat between mandibular rami; two large dark patches on throat. Photograph: Text Fig. 16.
- Lymnocyrtus minima*. Description: Bent, 1927: 104; Lowe, Bull. Brit. Ornith. Club 55: 43-44, 1934*.
- Limnodromus griseus*. Description: Pitelka, U. Calif. Publ. Zool. 50: 12, Table 5, 1950*. Photograph: Pitelka, *op. cit.*, Pl. 10; Text Fig. 15. (Note: The description by Witherby *et al.*, 1940: 212, refers to *scolopaceus*; this error may be traced to Bent, 1927: 110, who mistakenly assumed that the downy plumages of both species were identical.)
- Limnodromus scolopaceus*. Description: Rowan, Brit. Birds 20: 215, 1927; Bent, 1927: 118-119*; Pitelka, U. Calif. Publ. Zool. 50: 12, Table 5, 1950*. Photograph: Pitelka, *op. cit.*, Pl. 10. Drawing: Rowan, *op. cit.*, p. 216. Color Plate: Brooks, Ibis 1939: Pl. 8 (opp. p. 450); Vorobiev, "Ptitsy Yakutii," Acad. Sci. U.S.S.R., (Moscow), Pl. 45, 46, 1963.
- Limnodromus semipalmatus*. Description: Hachlow, L'Oiseau et la Rev. Franc. d'Ornith. 2: 290, 1932. Color Plate: Hachlow, *op. cit.*, opp. p. 289.
- Subfamily CALIDRIDINAE**
- Aphriza virgata*. Description: Murie, Auk 41: 236, 1924; Bent, 1929: 273. Photograph: Wetmore *et al.*, "Water, Prey and Game Birds of North America," p. 324, 1965 (color); Text Fig. 13.
- Calidris tenuirostris*. Description: Portenko, Arctica 1: 82-84, 1933. Photograph: Portenko, *op. cit.*, p. 87. Color Plate: Portenko, *op. cit.*, opp. p. 96.
- Calidris canutus*. Description: Bent, 1927: 138*; Witherby *et al.*, 1940: 231; Snyder, "Arctic Birds of Canada," p. 151, 1957. Photograph: Bridgman, Nat. Hist. 19: 75, 1919. Color Plate: Dalgety *et al.*, Ibis 1931: Pl. 10 (opp. p. 255); Pleske, "Birds of the Eurasian Tundra," Pl. 36, 1928.
- Calidris alba*. Description: Witherby *et al.*, 1940: 280; Snyder, "Arctic Birds of Canada," p. 184, 1957. Photograph: Bent, 1927: Pl. 45. Color Plate: Dalgety *et al.*, Ibis 1931: Pl. 10 (opp. p. 255); Pleske, "Birds of the Eurasian Tundra," Pl. 34, 1928.
- Calidris pusilla*. Description: Ridgway, 1919: 211*; Bent, 1927: 247-248; Snyder, "Arctic Birds of Canada," p. 174, 1957. Photograph: Dixon Bird Lore 19: 189-190, 1917.
- Calidris mauri*. Description: Ridgway, 1919: 215-216*; Bent, 1927: 259*. Photograph: Bent, 1927: Pl. 43.
- Calidris ruficollis*. Description: Ridgway, 1919: 291; Bent, 1927: 216; Gladkov, J. f. Ornith. 98: 200, 1957. Gladkov, *op. cit.*, Pl. 3 (opp. p. 196).
- Calidris minuta*. Description: Witherby *et al.*, 1940: 248; Portenko, J. f. Ornith. 100: 167, 1959. Color plate: Gladkov, J. f. Ornith. 98: Pl. 3 (opp. p. 196), 1957.
- Calidris subminuta*. Apparently undescribed.
- Calidris minutilla*. Description: Ridgway, 1919: 295*; Bent, 1927: 205.
- Calidris fuscicollis*. Description: Bent, 1927: 185; Snyder, "Arctic Birds of Canada," p. 161, 1957. Photograph: Bent, 1927: Pl. 32. Color Plate: Sutton in Parmelee *et al.*, Wilson Bull. 80: 4, 1968.
- Calidris bairdii*. Description: Ridgway, 1919: 280*; Bent, 1927: 196-197; Snyder, "Arctic Birds of Canada," p. 164, 1957.
- Calidris melanotos*. Description: Ridgway, 1919: 270*; Bent, 1927: 174-175*; Witherby *et al.*, 1940: 262. Photograph: Bent, 1927: Pl. 30. Color Plate: Brooks, Ibis 1939: Pl. 8 (opp. p. 450); Portenko, J. f. Ornith. 100: Pl. 2 (opp. p. 150), 1959.
- Calidris acuminata*. Description: Vorobiev, "Ptitsy Yakutii," Acad. Sci. U.S.S.R. (Moscow), p. 109-113, 1963. Color Plate: Vorobiev, *op. cit.*, Pl. 41.
- Calidris maritima*. Description: Ridgway, 1919: 240-241; Witherby *et al.*, 1940: 275-276; Snyder, "Arctic Birds of Canada," p. 154, 1957. Drawing: Sutton, "Iceland Summer," p. 79, 1961.
- Calidris ptilocnemis* subsp. Description: Conover, Zool. Ser. Field Mus. Nat. Hist. 29 (1): 172 (*ptilocnemis*), 174 (*couesi*), 177 (*tschuktschorum*), 178 (*quarta*), 1944. Photograph: Bent, 1927: Pl. 27; Bailey, "Birds of Arctic Alaska," p. 214, 1948: Text Fig. 18.
- Calidris alpina*. Description: Ridgway, 1919: 258; Witherby *et al.*, 1940: 237-238; Snyder, "Arctic Birds of Canada," p. 168, 1957. Color Plate: Witherby *et al.*, 1940: Pl. 109 (opp. p. 232).
- Calidris ferruginea*. Description: Witherby *et al.*, 1940: 243; Portenko, J. f. Ornith. 100: 164, 1959. Color plate: Portenko, *op. cit.*, Pl. 2 (opp. p. 150).
- Eurynorhynchus pygmeus*. Description: Ridgway, 1919: 305; Bent, 1927: 242. Photograph: Portenko, J. f. Ornith. 98: Pl. 16 (opp. p. 463); Text Fig. 18. Color Plate: Thayer, Auk 28: Pl. 2 (opp. p. 152; shows head only).
- Limicola falcinellus*. Description: Witherby *et al.*, 1940: 293. Photograph: Text Fig. 18. Color Plate: Vorobiev, "Ptitsy Yakutii," Acad. Sci. U.S.S.R. (Moscow), Pl. 42, 1963.
- Micropalama himantopus*. Description: Bent, 1927: 124; Snyder, "Arctic Birds of Canada," p. 171, 1957. Photograph: Text Fig. 19.
- Tryngites subruficollis*. Description: Brooks, Ibis 1931: 451-452; Snyder, "Arctic Birds of Canada," p. 177-178, 1957. Photograph: Text Fig. 19. Color Plate: Brooks, Ibis 1939: Pl. 8

(opp. p. 450); Sutton, Arctic 20: 2, 1967.

Philomachus pugnax. Description: Ridgway, 1919: 220; Witherby *et al.*, 1940: 286. Photograph: Text Fig. 19. Color Plate: Witherby *et al.*, 1940: Pl. 112 (opp. p. 280).

Superfamily CHIONIDOIDEA

Family THINOCORIDAE

Attagis gayi. Description: AMNH no. 447323. Locality unstated.

Head, face, neck, and chest, grayish brown, irregularly mottled with fine brownish-black markings. Back grayish brown with broad brownish-black midback stripe; two narrower dark stripes appear to roughly parallel the central stripe, but their configuration is not clear, due to the make of the skin. Wing dark to wrist, mottled grayish distally. Throat, belly, buffy gray. Photograph: Text Fig. 25.

Attagis malouinus. Description. AMNH no. 444304. Brecknock Island, Chile. Similar to *A. gayi* but ground color of dorsal down yellower; down on venter whitish with faint buffy tinge, darkest on throat and chest. Head with dark crown patch from which three broad stripes extend onto occiput; small dot on lores and at base of upper mandible; face, neck, finely mottled with dark brown. Wings yellowish buff with broad dark stripe paralleling ulna. Back streaked with dark brown in no apparent pattern. Photograph: Text Fig. 25.

Thinocorus orbignyianus. Description: AMNH no. 182383. Puente del Inca, Argentina. Head, back, wings, flanks, light buff, lightly though uniformly covered with whitish, dark brown flecking. Inverted dark brown V-shaped figure on back. Head pattern consists of dark central stripe from base of upper mandible to crown flanked by two short, parallel, supraorbital stripes; dot on lores; short malar stripe; rest of face lightly mottled. Venter dirty white with buffy tinge, darkest on belly. Photograph: Text Fig. 25.

Thinocorus rumicivorus. Description: BMNH no. 1902.3.13.1736. San Lorenzo Island, Peru. Similar to *T. orbignyianus* but paler, much more heavily dotted with white-tipped down. Brown down forms a solid crown patch and a broad central stripe on the lower back, but these areas are masked by the heavy whitish stippling. Face whitish, narrow whitish supraorbital line. Venter whitish with faint buffy tinge. Photograph: Text Figs. 25, 26.

Family CHIONIDIDAE

Chionis alba. Description: Clarke, Ibis 1906: 183; Bennett, Ibis 1926: 321; Jones, Brit. Antarctic Surv. Bull. 2: 67, 1963*. Color Plate: Clarke, Ibis 1906: Pl. 3, Fig. 2, (opp. p. 144).

Chionis minor. Description: Sharpe, 1896, 712. Studer, Int. Ornith. Cong., 3rd, Paris, 1900, p. 275-276, 1901.

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